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TEMPERATURE AND RATE OF MOISTURE INTAKE IN SEEDS[1]

CHARLES A. SHULL

(WITH FOUR FIGURES)

Introduction

Some years ago BROWN and WORLEY (1) published an account of some experiments dealing with the influence of temperature on the rate of moisture intake by seeds of barley. They found that the value of Q_{10} for the intake of water is high, approximating that of the van't Hoff law. They interpreted this as indicating that the rate of water absorption through a semipermeable membrane is conditioned by some chemical change which occurs as the temperature rises. In discussing the probable nature of this change they intimate that the water molecule is probably simplified as a result of the temperature rise. In doing so they in a measure accept ARMSTRONG'S hydrone theory of the structure of water. Cold water, according to this conception, is composed of complex molecules having at least several H_2O groups combined into a single molecule. These more complex molecules are supposed to break down into simpler groups as the temperature rises; the water becomes less viscous, and is able to penetrate the semipermeable coats of barley seeds more rapidly. The velocity of water intake

[1] Contributions from the Botanical Laboratories of the University of Kentucky, no. 1.

was calculated from the tangents of the curves of intake, using a string and protractor for measuring the tangents. This is a very crude and inaccurate method, especially in unskilled hands, but one easily used. They assert that the velocity of water absorption is almost exactly an exponential function of the temperature.

A short time previous to the appearance of this work the writer (3) had found that the seeds of *Xanthium* have semipermeable coats, and experiments on the influence of temperature on the rate of moisture intake by these seeds were in progress at about the time that BROWN and WORLEY'S paper appeared. The results of the work, however, did not receive careful mathematical consideration until about two years later, when it was found that the conclusions reached by BROWN and WORLEY from their work on barley seeds could not be drawn from the data which had been obtained from *Xanthium* seeds. A preliminary report of the work was made before the Botanical Society of America at the Columbus meeting in 1915. The data which had been obtained indicated that the value of Q_{10} was approximately 1.5, somewhat higher than the temperature coefficient of diffusion, but notably lower than that of chemical processes. This situation is very similar to that later reported by DENNY (2) for the effect of temperature on the rate of permeability of certain plant membranes to water.

Shortly following the Columbus meeting a few tests were run on seeds of *Xanthium* having a somewhat different environmental history. Mainly, the seeds were older than those previously used. The intake curves did not check very well with the former data, and it was thought desirable to repeat the experiments with seeds of the same species of *Xanthium* but of different genetic origin and environmental history. In this way it was felt that data might be obtained regarding the variability in the rate of water absorption in these seeds. The data which have been accumulated have been subjected to a critical analysis, principally to insure accuracy in the measurements of tangents. At the same time the possibility of a rate law has been kept in mind; but from a study of absorption in a number of cases I have decided that it would be unsafe or at least premature to propose a rate law on the basis of data now obtained. At the same time, the formulae presented may have

rather wide application, and deserve to be considered by those interested in the problems of absorption. While on the theoretical side certain features of the work have been disappointing, it will be worth while to give a somewhat detailed account of the experiments, as a contribution to our knowledge of the facts concerning the intake of water by dry organized matter.

I wish to acknowledge my indebtedness to Professor S. P. SHULL for valuable assistance with the mathematical part of the work. He has given generously of his time during the last five years to a painstaking analysis of the data, which has made possible a degree of accuracy otherwise unobtainable, and without which the general significance of the data could not have been fully appreciated. He has also tested many hypotheses as to the influence of factors upon intake rates. The principal part of the experimental work was done in the Laboratory of Plant Physiology at the University of Kansas, and part of it at the University of Chicago during the summer of 1914. The privileges of the Hull Botanical Laboratory for this work were much appreciated.

Materials and methods

The experiments were carried on with the lower seeds of *Xanthium pennsylvanicum* Wallr., and the naked cotyledons of several varieties of peas, the Canada green field pea, the Tom Thumb garden pea, and the Small Scotch Yellow pea of commerce. The cockleburs were chosen for their semipermeable coats, and the peas because the elimination of coat effects is easy. At first seeds of *Xanthium* were collected in the field; but these were soon replaced by pure line seeds grown on the breeding grounds of the University of Kansas in 1913. It was felt that such seeds might be more valuable than those of mixed genetic origin, more uniform in behavior, and the absorption data therefore more susceptible to mathematical consideration. After it had become evident that age, environmental history, genetic origin, and other factors might influence the intake phenomena, seeds were obtained from plants growing near the writer's home in Lawrence, Kansas. Slight differences in the shape and appearance of the seeds of different plants indicated possible lack of genetic purity, although the

plants by all their external characteristics were unmistakably true *X. pennsylvanicum*. These were used in the later work to give an idea of the variability to be encountered in the moisture intake by a given kind of substance.

The absorption took place in test-tubes of distilled water which were kept at the desired temperature by standing them in a water bath. Care was taken, particularly in the later work, to have the seeds at the same temperature as the water when they were first brought together. Three temperature curves are discussed in the present paper, 5, 20, and 35° C. Tests were run at 5° intervals from 5° to 50° C., but these three stand near to the temperatures used by BROWN and WORLEY, and afford a satisfactory basis for comparison. The others have been omitted. In all cases the fluctuation rarely exceeded 0.25° on either side of the chosen temperature during the significant period of intake.

At close intervals the seeds were removed from the water, dried uniformly and quickly on filter paper, and weighed with analytical accuracy. The time periods of immersion were made as sharp and accurate as possible, and the time during which the seeds were out of the water was reduced to the lowest possible limit. The drying required 10–20 seconds usually, and the weighing was done as rapidly as accuracy permitted. During this period the seeds had some opportunity to change from the temperature of absorption in the 5° and 35° tests, but histeresis of the seed colloids would tend to prevent serious alterations in colloidal aggregation during the brief interval involved. The errors due to such changes would be slight. The intervals between weighings were made short throughout the work. The first weighing was always made at the end of 1 minute to catch the very rapid initial intake. Succeeding intervals were usually 10 or 15 minutes, or longer when continuous attention could not be given to the work. The time intervals used will always be indicated in the tables with the absorption data. In all cases the time needed for drying and weighing was subtracted. This weighing at intervals was continuous in the case of *Xanthium* seeds until the intake was well above 35 per cent out of a possible 50–55 per cent. By the time 40 per cent of water had been taken in, the velocity of intake always

showed marked and increasing depression, due to approaching saturation. The split peas take up a considerably larger percentage of water than *Xanthium* seeds, and the intervals were continued until intake significant for the problem in hand had ceased.

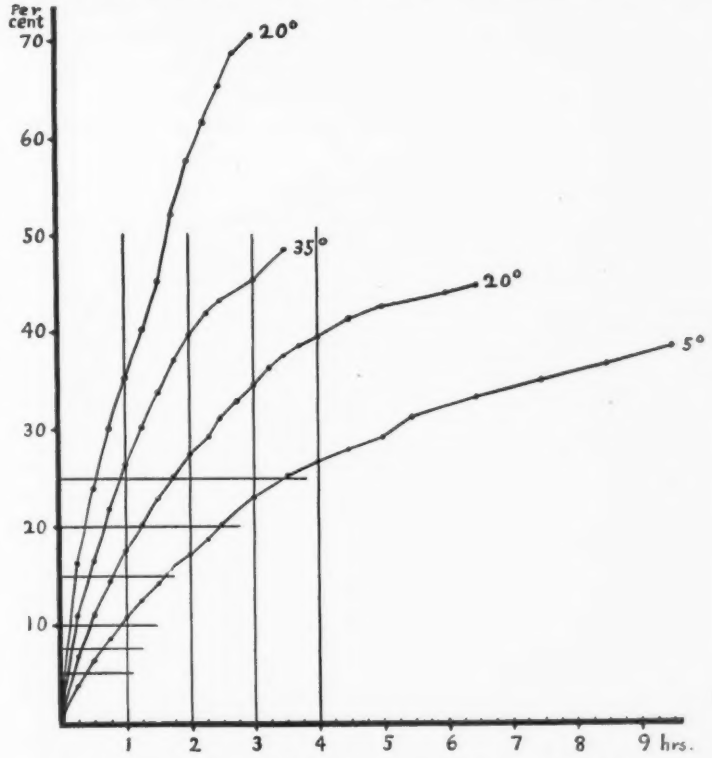

FIG. 1.—Curves of moisture intake: lowest curves, 5, 20, and 35°, by *Xanthium* seeds; upper curve, split peas, 20°; horizontal lines show points of equal intake where tangents were measured.

The value of close time intervals, despite certain obvious disadvantages, will be indicated later in discussing the work of BROWN and WORLEY.

The velocity of intake at any given moment has been calculated from the tangents to the curves. By reference to fig. 1 it will be

seen that horizontal lines cut the three temperature curves for *Xanthium* seeds at 5, 7.5, 10, 15, 20, and 25 per cent of intake. The tangents were determined at the points where these horizontal lines of equal intake cut the curves. From the velocity of intake at the three points cut by each horizontal line, the ratios of velocity have been derived, and from these ratios the mean value of Q_{10}.

The string and protractor method of measuring tangents was found to be too crude and inaccurate, especially where the angle of the tangent is high. The English investigators, however, used the method with fair success. Their measured tangents deviate but slightly from tangents calculated accurately for the same points in their curves, but in less skilful hands serious error might occur. In this work all tangents have been calculated from the known algebraic formulae of the curves, and all inaccuracy of measurement has been thereby eliminated.

In some cases data have been discarded, but only when it was entirely justified, and necessary from the mathematical standpoint. Whenever during the course of an experiment any of the seed coats became ruptured, the curve of intake was distorted because the surface of intake was greatly increased. Mathematical analysis of such data is impossible or meaningless. Such series of data have been discarded, and only those have been used which went through the many dryings and weighings without injury.

Experimental data

The data presented in table I were obtained with seeds from the first generation of a pure line of *Xanthium pennsylvanicum* Wallr., from the same line as was used for work on soil moisture published previously (**4**). The general characters of the type used have been described as type II in a discussion (**5**) of physiological isolation in the genus. The series of data chosen for mathematical consideration were drawn from a large mass of data some time before the analysis was made, solely on the basis of maintenance of satisfactory conditions during the period of observation. Ten lower seeds of *X. pennsylvanicum* were used in each case.

The series at any given temperature were fairly uniform with these seeds at the time the work was done. The variability to

be encountered is illustrated very well by the duplicate tests presented for 5° C.

The earlier work on split peas was not very satisfactory. They are more difficult to dry uniformly, and small pieces are more easily lost from the edges of the cotyledons during the drying, especially at higher temperatures. In table II data are given for two tempera-

TABLE I

WATER INTAKE OF *Xanthium* SEEDS IN PERCENTAGE OF AIR-DRY WEIGHT

TIME	5°		20°	35°
	I	II	I	I
1 minute	1.124	1.36	1.73	2.45
15 minutes	3.814	4.23	6.806	10.89
30 minutes	6.226	6.18	11.00	16.41
45 minutes	8.544	8.32	14.55	21.81
60 minutes	10.747	9.92	17.38	26.38
75 minutes	12.521	11.90	20.20	30.21
90 minutes	14.202	13.05	22.81	33.89
105 minutes	15.710	14.65	25.12	37.11
120 minutes	17.101	15.81	27.44	39.80
135 minutes	18.724	17.65	29.32	41.87
150 minutes	20.182	19.81	31.06	43.25
165 minutes	.....	20.90	32.80	.....
180 minutes	23.002	22.27	34.54	45.24
195 minutes	.....	23.40	36.13	.....
210 minutes	25.159	24.54	37.43	48.46
225 minutes	.....	26.54	38.52	.....
240 minutes	26.701	.....	39.39	.....
255 minutes	.....	27.96	.....	.....
270 minutes	27.965	.....	40.98	.....
290 minutes	.....	29.56	.....	.....
300 minutes	29.182	.....	42.57	.....
330 minutes	31.304	31.00	.....	.....
360 minutes	.....	.....	43.95	.....
390 minutes	33.159	.....	44.75	.....
450 minutes	35.072	.....	.....	.....
510 minutes	36.486	.....	.....	.....
570 minutes	38.400	.....	.....	.....
18.5 hours	45.020	.....	.....	.....
26 hours	.....	.....	47.28	.....

tures only, 20 cotyledons being used for each measurement. Curves of intake have been plotted for the cocklebur seeds at all three temperatures, and for the split peas at 20° C. in fig. 1. The split peas are included here merely to show how various substances differ in rate of intake at the same temperature. The rate of

intake, of course, varies with physical structure, chemical composition, state of aggregation of colloids, etc.

TABLE II

WATER INTAKE OF COMMERCIAL SPLIT PEAS (VARIETY UNKNOWN) IN PERCENTAGE OF AIR-DRY WEIGHT

Time	20°	35°
1 minute	4.25	5.30
15 minutes	16.20	20.83
30 minutes	23.84	33.04
45 minutes	30.14	41.94
60 minutes	35.32	50.30
75 minutes	40.30	57.60
90 minutes	45.22	63.77
105 minutes	52.06	67.81
120 minutes	57.50	71.00
135 minutes	61.42	.....
150 minutes	65.34	.....
165 minutes	68.66	74.32
180 minutes	70.32	.....
195 minutes	72.18	.....
210 minutes	72.97	.....
285 minutes	.....	76.11
330 minutes	74.96	.....
22 hours	.....	77.50
22.5 hours	74.96	.....

TABLE III

WATER INTAKE BY *Xanthium* SEEDS IN PERCENTAGE OF AIR-DRY WEIGHT, 5° C.

Time (minutes)	I	II	III	IV	V	Percentage of averages
1	1.30	1.90	1.33	2.19	1.57	1.64
5	3.29	3.25	3.70	3.87	3.33	3.44
10	4.74	4.47	5.25	5.92	4.90	4.97
15	6.20	5.55	6.88	6.87	6.15	6.22
30	8.49	8.13	9.02	9.72	8.92	8.72
45	10.79	10.43	11.09	11.76	10.87	10.82
60	12.85	11.79	13.02	13.00	12.81	12.50
90	15.68	14.50	15.53	16.73	15.89	15.43
120	18.36	16.87	18.05	18.85	18.09	17.77
150	21.04	18.97	20.56	20.67	20.29	19.99
180	22.88	20.73	22.71	22.42	22.30	21.86
240	26.55	24.39	25.89	26.08	26.26	25.42
300	30.22	27.51	28.99	29.07	29.71	28.67
360	33.59	30.28	32.03	31.92	32.91	31.67
420	37.18	32.25	34.91	35.14	35.30	34.55
540	40.93	36.86	39.20	39.96	40.70*	38.56

* During the last two hour period in no. V the mean temperature was about 6.2° C.

After the earlier work had been analyzed, some tests were made on old seeds remaining on hand, in an effort to check up the initial

absorption rates. As the seeds seemed to show a somewhat different behavior, tending to decreased intake rates at the start, it was

TABLE IV

WATER INTAKE BY *Xanthium* SEEDS IN PERCENTAGE OF AIR-DRY WEIGHT, 20°C.

Time (minutes)	I	II	III	IV	V	VI	Percentage of averages
1	1.77	1.95	3.32	2.35	2.72	2.08	2.38
5	4.60	5.28	6.15	5.56	5.44	4.94	5.34
10	6.76	8.21	8.59	8.26	8.21	7.41	7.94
15	8.44	11.44	10.45	11.07	10.28	10.27	10.32
30	11.79	13.88	14.69	14.98	16.51	16.51	14.64
45	15.10	17.15	17.97	18.83	22.15	20.68	18.54
60	17.64	20.33	20.51	21.53	23.84	23.67	21.13
75	19.94	22.29	22.95	24.29	26.90	26.27	23.64
90	21.81	24.63	25.78	26.79	29.18	28.87	26.04
105	23.78	26.88	27.56	29.19	31.21	31.21	28.17
120	25.89	28.84	29.88	31.10	32.59	33.42	30.14
135	28.00	31.33	31.69	32.95	34.47	35.63	32.16
150	29.53	32.50	33.20	34.30	36.10	37.84	33.72
165	31.35	34.31	34.56	35.75	37.09	39.27	35.20
180	32.89	35.48	35.84	37.20	38.77	40.96	36.66
195	34.32	36.46	36.91	38.11	39.61	42.46	37.77
210	.....	37.54	37.79	39.01	40.50	43.69	38.79
225	.....	.....	38.86	40.01	41.44	44.73	.....
240	37.68	.....	39.45	40.86	42.33	45.77	40.64
300	40.27	41.84	41.55	44.56	.....	.....	.....

TABLE V

WATER INTAKE BY *Xanthium* SEEDS IN PERCENTAGE OF AIR-DRY WEIGHT, 35° C.

Time (minutes)	I	II	III	IV	V	VI	VII	VIII	Percentage of averages
1	2.21	2.46	3.73	2.84	2.46	2.75	3.76	2.44	2.83
5	6.35	7.37	9.28	7.61	5.88	6.19	9.92	7.04	7.46
10	10.22	11.37	15.40	11.34	9.78	10.25	14.98	11.10	11.82
15	14.23	14.59	20.24	14.25	12.31	12.79	18.47	13.80	15.11
20	16.85	17.36	23.13	17.15	14.09	15.34	21.41	16.51	17.84
30	21.28	22.58	27.77	21.85	19.49	19.95	25.44	21.25	22.45
40	25.14	26.42	31.94	25.45	23.67	23.52	28.86	25.44	26.32
50	28.80	30.18	34.90	29.25	27.09	26.82	31.81	26.69	29.70
60	32.39	33.79	37.66	32.85	30.16	30.12	34.68	31.94	32.95
70	35.15	36.64	40.01	35.20	33.11	33.29	37.21	35.05	35.71
80	37.29	39.48	42.23	37.76	35.50	36.31	39.33	37.21	38.13
90	39.23	41.78	44.05	39.70	37.62	38.79	41.18	39.24	40.19
100	39.50	43.78	45.53	41.22	39.67	40.92	42.75	41.00	41.78

felt that studies should be made of absorption in ordinary field material, with the purpose of disclosing the variability likely to occur at a given age of seeds. These experiments were conducted

through a period of several weeks on seeds ripened for about three months. To reduce the time element in drying and weighing, only two seeds were used in each test. At the same time care was taken to have the temperature of seeds and water equal at the beginning of the measurements in each test. Table III shows the results of

TABLE VI

WATER INTAKE IN SPLIT PEAS IN PERCENTAGE OF AIR-DRY WEIGHT

Time (minutes)	Tom Thumb Yellow			Green Canada field pea			Small Scotch Yellow		
	5°	20°	35°	5°	20°	35°	5°	20°	35°
1	3.00	3.76	4.38	3.17	4.09	5.54	1.77	5.38	5.77
5	7.28	8.60	10.19	7.98	9.20	14.01	7.26	13.26	16.34
10	10.48	12.63	14.90	11.73	13.49	20.30	11.50	19.98	26.54
15	13.05	15.50	18.69	14.61	16.68	25.62	15.58	25.09	33.65
20	.....	.....	22.10	.....	.....	30.94	.....	.....	41.54
30	16.79	21.15	27.78	19.33	22.98	41.59	22.48	33.69	54.23
40	.....	.....	32.24	.....	.....	52.33	.....	.....	63.75
45	20.02	26.16	.....	23.08	28.78	.....	26.64	.....	.....
48	.....	.....	.....	.....	.....	.....	.....	43.01	.....
50	.....	.....	36.78	.....	.....	68.24	.....	.....	69.04
60	22.83	30.11	42.34	26.35	34.96	80.40	29.82	50.89	73.56
70	.....	.....	50.34	.....	.....	89.36	.....	.....	74.04
75	25.67	33.33	.....	29.23	42.52	.....	36.37	58.24	.....
80	.....	.....	59.05	.....	.....	92.73	.....	.....	.....
90	28.09	37.28	64.27	32.31	50.41	94.68	40.00	69.59	.....
100	.....	.....	68.69	.....	.....	96.25	.....	.....	.....
105	30.58	45.34	.....	35.91	64.76	.....	43.37	68.10	.....
120	33.00	51.61	.....	38.17	73.96	.....	45.66	70.34	.....
135	.....	57.21	.....	.....	79.48	.....	48.85	72.58	.....
150	36.81	62.01	.....	43.89	82.99	.....	51.86	.....	.....
165	.....	67.16	.....	.....	.....	.....	54.07	.....	.....
180	40.79	70.74	.....	48.94	.....	.....	.....	.....	.....
210	44.92	.....	.....	55.10	.....	.....	.....	.....	.....
225	.....	.....	.....	.....	.....	.....	61.59	.....	.....
240	49.40	.....	.....	66.87	.....	.....	.....	.....	.....
270	54.42	.....	.....	68.22	.....	.....	.....	.....	.....
300	60.19	.....	.....	72.60	.....	.....	.....	.....	.....
330	66.11	.....	.....	.....	.....	.....	.....	.....	.....
345	.....	.....	.....	.....	.....	.....	69.91	.....	.....
360	71.87	.....	.....	.....	.....	.....	.....	.....	.....
390	73.67	.....	.....	.....	.....	.....	.....	.....	.....

five experiments at 5° C. In the last column is shown the percentage of the averages of intake. This percentage of the averages must not be confused with the average of the percentages, which would give a slightly different set of figures. In analyzing these variable groups we have used the percentage of the averages in attempting to construct a mathematical curve that would follow

the data. Similar groups of data for 20° and 35° C. are shown in tables IV and V.

The absorption data for the split peas were found on examination to be very difficult to analyze, owing to changes in rate of absorption, due almost certainly to internal physical changes in the seed. No attempt was made to carry out the work in so detailed a manner as in the case of *Xanthium* seeds. Enough has been done, however, to make it worth while to put the data on record. The results with three named varieties of peas at the three chosen temperatures are given in table VI.

Mathematical discussion

For purposes of mathematical discussion it is not considered essential to plot any curves of the data in addition to those given in fig. 1. Only such curves are used as are necessary to an understanding of the discussion. Anyone desiring the curves can easily plot them from the data.

In view of the fact that BROWN and WORLEY considered the curves of water absorption in *Hordeum* seeds as paraboloid running out toward a common asymptote, attention was turned first to the type of curve which would most nearly fit the data shown in the preceding tables. Even a casual examination of the data of tables I and II shows that the curves are not simple ones. Since the situation is somewhat simpler in the case of *Xanthium* seeds than in the split peas, the data from the former will be considered first.

XANTHIUM SEEDS

During the first moments of absorption (40–60 seconds) the entrance of water is exceedingly rapid; but in a short time the rate breaks sharply to a lower rate, which then decreases slowly but rather steadily during the main part of absorption, until approaching saturation begins to affect the rapidity of intake. In *Xanthium* seeds saturation occurs at about 50 per cent, and the final break in the curve caused by approaching saturation manifests itself at about 35–40 per cent, as is shown in the figures. The whole curve is thus apparently a composite curve made

up of at least three component curves. The general relations of these to one another in the composite curve are shown graphically in fig. 2, which has been somewhat exaggerated, especially in respect of the first curve, for the sake of clearness. The effect of the initial rapid intake is to throw the main part of the curve upward from the base line. Careful examination showed that it was not possible to find a parabolic curve that would follow the data at any temperature. The problem then was to find an empirical formula or equation or such a combination of equations as would very closely approximate the given data of observation. This was necessary

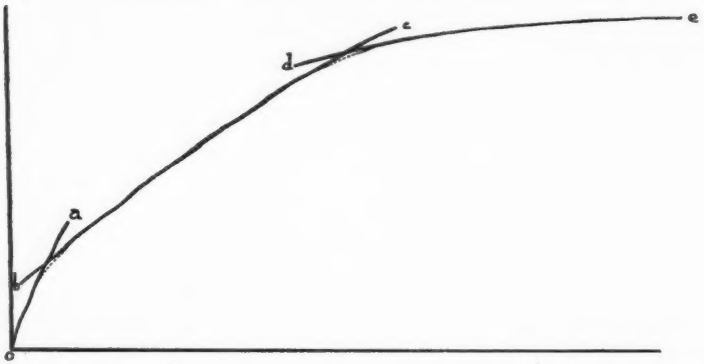

FIG. 2.—Curves showing composite nature of moisture intake curves in *Xanthium:* first curve exaggerated; *oa*, initial intake; *bc*, main curve; *de*, approaching saturation.

in order that precise and accurate methods of measuring tangents could be substituted for the uncertainties of the graphic method used by BROWN and WORLEY. The only proof we have that any equation or group of equations is adapted to such use lies in a comparison of the experimental data with corresponding values computed from the equation under consideration. As it is impossible to avoid slight irregularities in obtaining data, the equation must be so determined as to distribute the irregularities rather evenly on either side of the curve, as one would expect from the laws of chance variation.

Early in the investigation an equation was discovered which could be made to approximate very closely the series of data

obtained by measuring the total increase in weight due to absorption for different periods of immersion. This equation takes the form $y=a \log_{10}(bx+1)+c$, in which $y=$the total percentage of intake, and $x=$the length of time of immersion, a, b, and c being constants. In the later work it was found that a still closer approximation could be obtained by the employment of two equations of this form tangent to each other, the first equation representing the

TABLE VII

ALGEBRAIC CURVE FOR ABSORPTION DATA AT 5° C.; ABSORPTION IN PERCENTAGE OF AIR-DRY WEIGHT (*Xanthium*)

Time	Data low	Computed	Data high
1 minute	.....	1.055	1.124
15 minutes	.....	3.739	3.814
30 minutes	6.226	6.279	.....
45 minutes	8.544	8.545	.....
60 minutes	.....	10.591	10.747
75 minutes	.....	12.456	12.521
90 minutes	.....	14.169	14.202
105 minutes	15.710	15.753	.....
120 minutes	17.101	17.226	.....
135 minutes	.....	18.603	18.724
150 minutes	19.810*	19.896	.....
165 minutes	20.900*	21.113	.....
180 minutes	.....	22.265	22.270*
195 minutes	.....	23.356	23.400*
210 minutes	.....	24.394	24.540*
240 minutes	.....	26.327	26.701
270 minutes	27.965	28.098	.....
300 minutes	29.182	29.732	.....
330 minutes	.....	31.247	31.304
390 minutes	33.159	33.987	.....
450 minutes	35.072	36.410	.....
510 minutes	36.486	38.583	.....
570 minutes	38.400	40.524	.....
18.5 hours	45.020	52.975	.....

* Data from series II.

earlier data, the second representing the later data beyond the point of tangency. In one case it was found advantageous to introduce a third equation of this kind. The closeness with which this equation can be made to approximate the experimental data is truly surprising. It has been applied to the data furnished by BROWN and WORLEY for barley seeds, and approximates their data more closely than the calculated values they obtained from their formula. It must not be supposed, however, that the formula

can be successfully applied to all cases of absorption, or that it has any special significance beyond its applicability to measuring tangents accurately in all curves to which it fits.

In dealing with the data of table I it was found desirable to partially combine the two series at 5° C. because of irregularities in each set. As the seeds used in these early tests were not reduced to water temperature before immersion, some tests were run for

TABLE VIII

ALGEBRAIC CURVES FOR ABSORPTION DATA; INTAKE IN PERCENTAGE OF AIR-DRY WEIGHT (*Xanthium*)

TIME	20° C			TIME	35° C		
	Data low	Computed	Data high		Data low	Computed	Data high
1 minute	1.73	1.821	.....	1 minute	2.45	2.840	.....
15 minutes	.....	6.481	6.806	15 minutes	.....	10.136	10.89
30 minutes	.....	10.599	11.00	30 minutes	16.41	16.471	.....
45 minutes	.....	14.213	14.55	45 minutes	.....	21.720	21.81
60 minutes	17.38	17.396	.....	60 minutes	.....	26.317	26.38
75 minutes	20.20	20.239	.....	75 minutes	30.21	30.305	.....
90 minutes	.....	22.809	22.81	90 minutes	.....	33.855	33.89
105 minutes	25.12	25.153	.....	105 minutes	.....	37.054	37.11
120 minutes	.....	27.308	27.44	120 minutes	39.80	39.964	.....
135 minutes	.....	29.301	29.32	135 minutes	41.87	42.635	.....
150 minutes	31.06	31.157	.....	150 minutes	43.25	45.102	.....
165 minutes	32.80	32.891	.....	180 minutes	45.24	49.534	.....
180 minutes	.....	34.520	34.54	7 hours	48.46	72.348	.....
195 minutes	.....	36.056	36.13				
210 minutes	37.43	37.507	.....				
225 minutes	38.52	38.884	.....				
240 minutes	39.39	40.194	.....				
270 minutes	40.98	42.634	.....				
300 minutes	42.57	44.871	.....				
330 minutes	43.95	46.934	.....				
360 minutes	44.75	48.849	.....				
26 hours	47.28	84.280	.....				

corrections of initial intake with seeds at water temperature. The result was a slight lowering of the initial intake at 5° C., and an increase at 35° C. These corrections were taken into consideration in deriving the values of the constants for computing the theoretical intake from the formula.

In the 5° C. curve the values for the constants a, b, and c in the equation given are as follows: $y=48.5 \log_{10} (0.098x+1)+0.85$. The closeness of the intake computed from this equation to the actual data is illustrated in tables VII and VIII.

The computed intake agrees very well with the experimental data until the absorption reaches 33 per cent, and from that on the data fall more and more below the computed values. This falling off of the actual intake marks the beginning of the effects of approaching saturation. It is evident that tangents to the curve may safely be computed up to about 35 per cent of intake, but beyond that point the tangents could not be used for comparisons of the rate of intake in different curves.

For the absorption at 20° C. the substituted values for the constants make the equation read $y = 61.5 \log_{10}(0.0136x+1)+1.46$, and the corresponding equation for 35° C. is $y = 74.5 \log_{10}(0.0184x+1)+2.25$. The closeness of the computed intake to the data of observation in each case is shown in table VIII.

In the 20° curve the effects of approaching saturation first manifest themselves at about 37.5 per cent, and in the 35° curve at about 40 per cent of intake. In each curve the computed values are strikingly close to the actual data. The uniformity of absorption and the agreement of the calculated intake to that observed has been a surprising feature of the work; and since the final break due to approaching saturation is always at or beyond 35 per cent, I have felt confident of accuracy in measuring tangents of the curves to that point.

In the later work the data could not be so satisfactorily represented by means of a single equation. By the use of two or three successive equations, however, each joined to its successor in a point of equal tangency, a very close agreement between calculated intake and experimental data was obtained. For the purpose of calculating tangents, and rates of intake, this composite curve is just as satisfactory as if it were developed from a single equation.

The 5° curve will be considered first. The three empirical equations used are as follows:

(1) $y = 14.3 \log_{10}(0.078x+1)+1.398$
(2) $y = 35.07 \log_{10}(0.0121x+1)+4.195$
(3) $y = 87.95 \log_{10}(0.0023x+1)+8.625$

The first two curves have equal tangents for $x = 35.35$, and the last two for $x = 150.89$ (minutes). The breaks in the curve

are very small. Thus, at the first break, in curve 1, $y=9.605814$; while in curve 2, $y=9.6056$ at the common point of tangency with curve 1. At this common point the two curves are only 0.000214 (per cent) apart. Similarly at the second break, for curve 2, $y=20.01634$, and for curve 3, $y=20.016284$, a break of only 0.000056 per cent. This combination curve runs remarkably close to the data of observation and gives perhaps the best series presented. The calculated and observed intake is shown in table IX. Data in last column, table III.

TABLE IX

ALGEBRAIC CURVES FOR ABSORPTION DATA; INTAKE IN PERCENTAGE OF AIR-DRY WEIGHT (*Xanthium*), 5° C.

Time (minutes)	Data low	Computed	Data high
1	1.64	1.86	.....
5	.....	3.44	.....
10	4.97	4.98	.....
15	.....	6.21	6.22
30	8.77	8.89	.....
45	.....	10.82	.....
60	12.50	12.51	.....
90	.....	15.42	15.43
120	17.77	17.86	.....
150	.....	19.96	19.99
180	.....	21.86	.....
240	.....	25.41	25.42
300	.....	28.67	.....
360	.....	31.67	.....
420	.....	34.46	34.55
540	38.56	39.46	.....

The data obtained with *Xanthium* seeds at 20 and 35° C. were given similar treatment. Two equations were used for the 20° data as follows:

(1) $y=23.77 \log_{10}(0.088x+1)+1.524$

(2) $y=57.13 \log_{10}(0.0132x+1)+6.616$

These two curves have tangents equal for $x=34.52$, at which point curve 1 has $y=15.931972$, and curve 2, $y=15.931732$, only 0.00024 per cent apart.

In the 35° data, also, two successive equations were used:

(1) $y=34.92 \log_{10}(0.0983x+1)+1.40$

(2) $y=73.05 \log_{10}(0.0286x+1)+6.53$

The point of equal tangency in these curves comes at $x = 22.91$, and at this point in curve 1, $y = 19.28409$, while in curve 2, $y = 19.28407$. The break therefore is only 0.00002 per cent. The agreement between computed and observed intake here is not quite so close as in the 5° curve, but is still very good (see table X, the data for which come from the final columns of tables IV and V).

It is apparent in these later results, just as in the earlier ones, that approaching saturation does not begin to interfere with absorption rates until 35–40 per cent of intake has occurred. It should be quite clear, also, that the equations employed run so

TABLE X

ALGEBRAIC CURVES FOR ABSORPTION DATA; INTAKE IN PERCENTAGE OF AIR-DRY WEIGHT (*Xanthium*)

TIME (MINUTES)	20°			TIME (MINUTES)	35°		
	Data low	Computed	Data high		Data low	Computed	Data high
1.....	2.38	2.39	.....	1.....	.....	2.82	2.83
5.....	.....	5.29	5.34	5.....	.....	7.46	.....
10.....	7.92	8.05	.....	10.....	.....	11.78	11.82
15.....	.....	10.21	10.32	15.....	15.11	15.14	.....
30.....	14.64	14.86	.....	20.....	17.84	17.89	.....
45.....	.....	18.18	18.54	30.....	.....	22.38	22.45
60.....	.....	21.09	21.13	40.....	.....	26.29	26.32
75.....	23.64	23.69	.....	50.....	29.70	29.76	.....
90.....	.....	26.04	.....	60.....	.....	32.90	32.95
105.....	28.17	28.19	.....	70.....	35.71	35.75	.....
120.....	30.14	30.17	.....	80.....	38.13	38.37	.....
135.....	.....	32.00	32.18	90.....	40.19	40.79	.....
150.....	.....	33.71	33.72	100.....	41.78	43.03	.....
165.....	35.20	35.30	.....				
180.....	36.66	36.80	.....				

close to the observed data that the velocity of intake can be measured at any given moment with great accuracy. Instead of plotting curves and attempting to measure the tangents graphically, they have been calculated from the known formula.

The velocity of intake has been computed from the tangents for six points on each temperature curve of intake. These points coincide with those chosen by BROWN and WORLEY, as follows: 5, 7.5, 10, 15, 20, and 25 per cent of intake. The percentage hourly rate of intake for these points, on each curve shown in tables VII and VIII, together with the logarithms of the hourly rates of intake, are shown in table XI.

TABLE XI

WATER INTAKE IN *Xanthium* SEEDS

INTAKE PERCENTAGE	5°		20°		35°	
	Velocity in percentage per hour	Logarithm	Velocity in percentage per hour	Logarithm	Velocity in percentage per hour	Logarithm
$y=5$.....	10.1705	1.007342	19.0894	1.280792	32.8097	1.516002
$y=7.5$.....	9.0322	0.955794	17.3838	1.240145	30.3700	1.482445
$y=10$.....	8.0214	0.904250	15.8304	1.199492	28.1116	1.448886
$y=15$.....	6.3264	0.801157	13.1278	1.118191	24.0865	1.381774
$y=20$.....	4.9896	0.698066	10.8866	1.036893	20.6376	1.314659
$y=25$.....	3.9351	0.594956	9.0280	0.955592	17.6826	1.247546

In the later work the velocity calculated from the tangents is expressed in percentage per minute, instead of percentage per hour. The velocities for the same six points, on the curves shown in tables IX and X, are given in table XII.

TABLE XII

WATER INTAKE IN *Xanthium* SEEDS

INTAKE PERCENTAGE	5°		20°		35°	
	Velocity in percentage per minute	$\log_{10}$ Velocity	Velocity in percentage per minute	$\log_{10}$ Velocity	Velocity in percentage per minute	$\log_{10}$ Velocity
$y=5$.....	0.27122	$\bar{1}.433322$	0.64872	$\bar{1}.812057$	1.17576	0.070318
$y=7.5$.....	0.18134	$\bar{1}.258494$	0.50920	$\bar{1}.706888$	0.99707	$\bar{1}.998726$
$y=10$.....	0.12589	$\bar{1}.099992$	0.39968	$\bar{1}.601702$	0.84554	$\bar{1}.927134$
$y=15$.....	0.09066	$\bar{2}.957416$	0.24624	$\bar{1}.391358$	0.60806	$\bar{1}.783947$
$y=20$.....	0.06537	$\bar{2}.815378$	0.19096	$\bar{1}.280943$	0.44820	$\bar{1}.651472$
$y=25$.....	0.05722	$\bar{2}.757548$	0.15611	$\bar{1}.193431$	0.38284	$\bar{1}.583018$

TEMPERATURE COEFFICIENT.—Having now obtained the rate of intake at chosen points on each curve, we can proceed to determine the quantitative effects of temperature on the rate of moisture intake. First we must know the ratio of the velocity at 20° to that of 5° C., and of the velocity at 35° to that at 20° C. These ratios for the intake velocities presented in tables XI and XII are given in table XIII.

In the earlier data, represented by table XI, if we take the average velocity at 5° C. as unity, we have the comparative mean velocities at 20 and 35° C. according to the ratio $1:2.05:2.05\times 1.83=3.75$. Since the temperature of intake in the last curve

is 30° higher than the first, the mean value of Q_{10} will be obtained by extracting the cube root of the final term, 3.75, which is 1.55.

In the later data, table XII, the mean value of Q_{10} is higher. The final term of the ratio is 6.11, and its cube root 1.83. In both cases the value falls between the coefficient of temperature effects on physical and on chemical processes, but in the last case it approaches the van't Hoff coefficient. These figures are comparable with the value of Q_{10} obtained by BROWN and WORLEY for barley, as they have been obtained in exactly the same manner. The value of the temperature coefficient for *Hordeum* was 2.02.

BROWN and WORLEY considered that the velocity of intake was almost exactly an exponential function of the temperature. If it is,

TABLE XIII

RATIOS OF INTAKE VELOCITIES (*Xanthium*)

INTAKE PERCENTAGE	DATA TABLE XI		DATA TABLE XII	
	$\frac{\text{Velocity } 20°}{\text{Velocity } 5°}$	$\frac{\text{Velocity } 35°}{\text{Velocity } 20°}$	$\frac{\text{Velocity } 20°}{\text{Velocity } 5°}$	$\frac{\text{Velocity } 35°}{\text{Velocity } 20°}$
$y=$ 5.0.....	1.88	1.72	2.39	1.81
$y=$ 7.5.....	1.92	1.75	2.81	1.96
$y=$10.0.....	1.97	1.80	3.17	2.12
$y=$15.0.....	2.08	1.83	2.71	2.47
$y=$20.0.....	2.18	1.90	2.92	2.35
$y=$25.0.....	2.29	1.96	2.73	2.45
Mean ratios	2.05	1.83	2.79	2.19

logarithms of the velocities plotted against the temperature must lie in straight lines. They show in their second diagram such a plot of the logarithms, and state that the course of the lines in the diagram, in respect both of the straightness and of the agreement of inclination, furnishes evidence of a most conclusive character that the rate at which water is absorbed by barley seeds is an exponential function of the temperature. They call attention to the rarity with which physical properties show an exponential increase with rise in temperature, and then propose that the change is chemical and probably involves a simplification of the water molecule, as already stated.

The logarithms of the velocity of water intake by *Xanthium* seeds have been plotted similarly in fig. 3. The curves plotted

above the zero line represent the velocities for the earlier *Xanthium* data of table XI, while those below the zero line are from the later data from table XII. These curves will be discussed later.

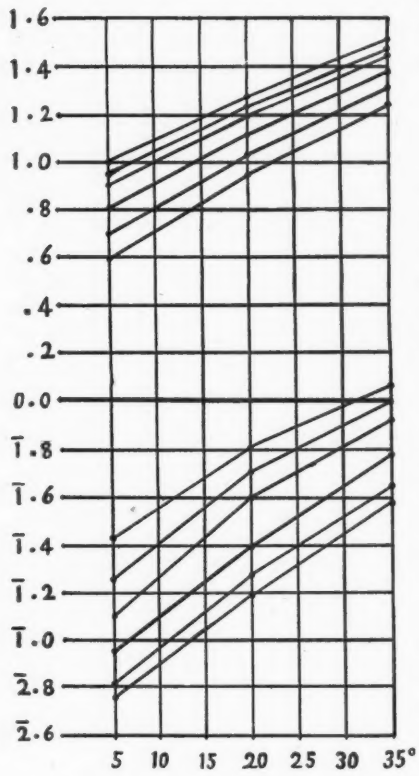

FIG. 3.—Logarithms of velocity plotted against temperature: upper series plotted from table XI, lower series from table XII; *Xanthium* seeds.

SPLIT PEAS

The split peas offered special difficulties from the mathematical side, and no attempt is made to present a complete account of the analysis of the data given in table VI. The variability of the data is much greater than in the case of cockleburs. The absorption is fairly consistent during the first hour, or, at high temperatures, during the first 15 or 20 minutes. After a certain critical percentage has been reached, however, they show a remarkable rise above the ideal curve indicated by the first part of the absorption. This critical percentage is about 20 per cent in the case of the Tom Thumb variety, about 23 per cent in the Canada Green field pea, and about 30 per cent for the Small Scotch Yellow commercial. The reasons for the rise in the rate of absorption will be considered in the general discussion.

As the Small Scotch Yellow gives us the longest period of consistent intake I shall present here data for this variety only,

and only for that portion of the curves which precedes the rise in rate.

Difficulties were encountered in choosing an empirical formula for the split pea data, owing partly no doubt to the fact that no duplicate tests were run, and the only set of data showed rather large irregularities at the beginning of the absorption. Curves closely approximating the data beyond 5 minutes ran below the point of origin. The one minute value ran quite too high in the 20 and 35° C. data, and somewhat too low in the 5° C. series. In any case the constant c in the formula was so small that it was thought best, after considering all possibilities, to run the com-

TABLE XIV

ALGEBRAIC CURVE FOR ABSORPTION DATA; SMALL SCOTCH YELLOW SPLIT PEA

TIME (MINUTES)	5°			20°			35°		
	Low	Computed	High	Low	Computed	High	Low	Computed	High
1...	1.77	1.81	.....	.....	3.75	5.38	.....	4.20	5.77
5....	.....	7.25	7.26	13.26	13.27	.....	16.34	16.41	.....
10....	11.50	11.88	.....	19.98	20.21	.....	.....	26.47	26.54
15....	.....	15.30	15.58	.....	24.93	25.09	33.65	33.73	.....
20....	.....	.....	.....	.....	.....	.....	.....	39.43	41.54
30....	.....	22.16	22.48	33.69	33.84	.....	.....	.....	.....
45....	.....	26.64	.....	.....	.....	.....	.....	Break up	.....
48....	.....	.....	.....	.....	40.30	43.01	.....	.....	.....
60....	29.82	29.97	.....	.....	Break up	.....	.....	.....	.....
75....	.....	32.62 Break up	36.37	.....	.....	.....	.....	.....	.....

puted curves through the point of origin, and omit that constant altogether. The generalized formula then takes the form $y = a \log_{10} (bx+1)$.

The three formulae, for the 5, 20, and 35° C. curves for the Small Scotch Yellow peas, with values of a and b substituted, are as follows:

$$5° \text{ C.}: y = 30.13 \log_{10} (0.148x+1)$$
$$20° \text{ C.}: y = 34.58 \log_{10} (0.284x+1)$$
$$35° \text{ C.}: y = 60.90 \log_{10} (0.172x+1)$$

Using these empirical formulae, we have secured a fair agreement between calculated and observed intake, not so close as in the case of *Xanthium*, but much closer than is frequently obtained

in attempts to reduce biological phenomena to mathematical expressions (see table XIV).

The velocity of intake at the same six percentages used for the *Xanthium* seeds has been calculated from the tangents to the curves. The velocity in percentage per minute, and the logarithms of the velocities are shown in table XV.

TABLE XV

WATER INTAKE IN SMALL SCOTCH YELLOW SPLIT PEA

INTAKE PERCENTAGE	5°		20°		35°	
	Velocity in percentage per minute	Log_{10} velocity	Velocity in percentage per minute	Log_{10} velocity	Velocity in percentage per minute	Log_{10} velocity
$y=5$	1.32160	0.121100	3.05728	0.485335	3.76544	0.575827
$y=7.5$	1.09175	0.038122	2.58846	0.413041	3.42593	0.534779
$y=10$	0.90188	$\bar{1}$.955148	2.19152	0.340745	3.11692	0.493725
$y=15$	0.61546	$\bar{1}$.789200	1.57091	0.196151	2.58002	0.411623
$y=20$	0.42000	$\bar{1}$.623249	1.12605	0.051558	2.13562	0.329524
$y=25$	0.28662	$\bar{1}$.457306	0.80717	$\bar{1}$.906965	1.76775	0.247421

The ratios of the intake velocities for the split peas were obtained from the data of table XV, and are presented in table XVI.

TABLE XVI

RATIOS OF INTAKE VELOCITIES; SMALL SCOTCH YELLOW SPLIT PEAS

Intake percentage	$\frac{\text{Velocity } 20°}{\text{Velocity } 5°}$	$\frac{\text{Velocity } 35°}{\text{Velocity } 20°}$
$y=5$	2.31	1.23
$y=7.5$	2.37	1.32
$y=10$	2.43	1.42
$y=15$	2.55	1.64
$y=20$	2.68	1.90
$y=25$	2.82	2.19
Mean ratio	2.53	1.62

From the mean ratios we find that the value of Q_{10} in this case is 1.6, or just a little higher than the earlier determination for *Xanthium*. Since the calculations in the case of split peas are made from single equation curves, all passing through the point of

origin, they offer the best possible opportunity to study the question of straight line plots of logarithms against temperature. These are shown in fig. 4. It is seen that they are decidedly not straight lines.

Having now presented in some detail the results of the mathematical analysis of the data, which has been carried out in such a way as to make possible a comparison between this work and that of BROWN and WORLEY, I shall discuss briefly the significance of the results.

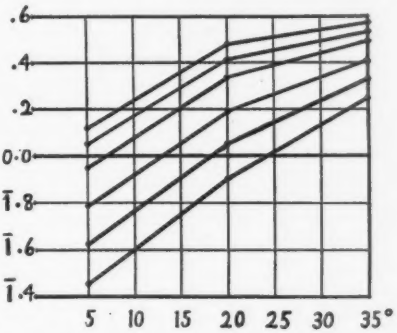

FIG. 4.—Logarithms of velocity plotted against temperature, split peas, table XV.

Discussion

There are several features of the work by BROWN and WORLEY which need to be considered in judging its value. Attention was called in the introduction to the rather rough method of securing tangents, which, however, was quite skilfully used. In view of the fact that the early phases of absorption were not studied by them, however, it is possible that the tangents they obtained between the point of origin and the first intake data at each temperature would not agree with those of a curve plotted at close intervals. If the barley seeds were to show a large initial intake, the curve would be thrown upward from the base, and the succeeding portion of the curve would have a different course, affecting the very portion of the curve where the tangents are measured in determining intake velocities. It is this early part of the curve which is important, for the tangents are measured for that part of the curve between the origin and 25 per cent of intake.

The greatest disadvantage in the data supplied by BROWN and WORLEY is the long time interval between observations, and especially the long first interval. Their first observations were taken at 5–6 hours after the beginning of absorption. If I had waited 5 hours for the first observations in any of the work presented

in this paper, all of the tangents used in measuring intake velocities would have fallen on that part of the curve between the point of origin and the first reading, all of which is constructed from imagination, as an "ideal curve." In the case of barley it is not so serious, but it is only in the 3.8° curve that all of the tangents fall beyond the first observation. In their 21.1° curve the first observation showed over 9 per cent of intake, from which it is seen that the 5 and 7.5 per cent tangents were measured on a "guess curve" between the origin and the first observation, and the 34.6° curve is still less favorable; for in it the first observation shows nearly 17 per cent of intake, so that 4 out of 6 tangents used were measured on a curve constructed entirely without data. This matter is vital to the whole theory they propose, for they had but three points in plotting logarithms of velocities against temperatures, and if one of the points is insecure no conclusions can be drawn. The other two points are bound to be in a straight line. In four cases out of six, the third point is not established by data, and in two of the plotted logarithm-temperature curves, both the second and the third points are derived from tangents whose determination is insecure. The evidence offered, therefore, that the velocity of intake is an exponential function of the temperature, is not very convincing. In this work I have used short time intervals to understand better the curve whose tangents were to be measured. Our short intervals have the disadvantage that water movement goes on in the seed during weighing which occurs frequently. There is no intake during weighing, of course, but distribution of water already taken in continues. I have felt that the advantages of the close intervals between weighings exceed by far any disadvantage that might exist.

In the case of *Xanthium*, with a semipermeable coat, and in split peas without the coat, I have found that the plotting of logarithms of velocity against temperatures does not yield straight lines. The nearest approach to straight lines is seen in the upper half of fig. 3, but even here there is a slight divergence, always in the same direction. A somewhat greater divergence from straight lines is seen in the lower half of fig. 3, and a very marked divergence is seen in fig. 4, in the case of split peas. From the data I conclude

that plotting logs of velocities against temperatures will yield some kind of a curve, but there are not enough data at hand to determine anything as to the character of the curve. The general conclusion to be drawn from this part of the work is that the evidence, as far as it goes, is rather against the assumption that the velocity of intake is an exponential function of the temperature.

Another point that deserves notice is the nature of the curves of water intake. BROWN and WORLEY called their curves paraboloid and described them as running out toward a common asymptote. The language, of course, must have been intended in a very loose sense, for parabolic curves passing through a common point of origin, as theirs do, could never have a common asymptote. It was found impossible to fit a parabolic formula to the intake data presented, but from the figures given in tabular form (tables VII–X and XIV) it is evident that the logarithmic curve $y=a \log_{10} (bx+1)+c$ may be made to fit the data very closely. Furthermore I have taken the 3.8° barley data and attempted to fit to it both the logarithmic and a hyperbolic equation made to pass through the origin and the second and fourth values of their data. I have found that the logarithmic equation fits much closer to their data than the hyperbolic equation. The two sets of values and the original data are given for comparison. The time and data columns are from BROWN and WORLEY.

Time	Data	Computed (logarithmic)	Computed (hyperbolic)
5.58 hours	4.42	4.41	5.21
24.75 hours	11.82	11.82	11.82
48.83 hours	18.52	18.49	17.99
72.25 hours	23.42	23.43	23.42
96.50 hours	27.42	27.56	28.78
144.25 hours	34.02	33.89	38.99

The logarithmic equation used in this comparison is $y=48.6 \log_{10} (0.025x+1)$, and the hyperbolic equation, $y=0.2024 \sqrt{x^2+112.988x}$.

Considering the closeness of agreement which is obtainable with the logarithmic formula, it seems more reasonable to consider the curves of water intake, even in the case of barley seeds, as logarithmic rather than hyperbolic.

If the velocity of absorption were an exponential function of the temperature, the relation between temperature and the rate of entry of water into the seeds might be expressed by an equation of the form $v = ae^{k\theta}$ in which θ is the temperature. As I have obtained evidence somewhat adverse to the assumption that velocity of absorption is an exponential function of the temperature, this equation does not hold. Wherever the logarithmic formula $y = a \log_{10}(bx+1)+c$ holds for the curves of absorption, the velocity of intake may be represented by the formula $v = ae^{-k\phi}$ in which ϕ is the percentage of water already absorbed. In other words, the velocity of intake is approximately an inverse exponential function of the total preceding absorption. It is not claimed that this is true for all cases of absorption, but that it is just as true as the logarithmic equation used. Wherever that equation holds, the velocity formula holds.

The chief interest centers in the temperature coefficient of absorption. I have obtained coefficients ranging from 1.55 to 1.83 in *Xanthium* seeds, and 1.6 in split peas. These are all above the temperature coefficient of physical changes, and below that for chemical change. BROWN and WORLEY obtained a value above 2, and adopted the idea that absorption was conditioned as to rate, in the case they studied, by some chemical change. In seeking a chemical change to account for their observations, they suggested that the semipermeable seed coat of barley was involved in a special way, in its relation to complex or simplified water molecules. They suggested the possibility that the differential septum (semipermeable coat) permits only hydrone to penetrate it, and that the temperature rise increases the proportion of hydrone in solution. One of the main difficulties in the way of accepting such a hypothesis as to the relation of hydrone to semipermeable membranes, is its implication that all semipermeable membranes should behave alike. *Xanthium* and *Hordeum* both have semipermeable membranes, and if the rate of water passage depended solely on the proportion of hydrone, treatment of either seed should give the same results. It is a notable fact, however, that semipermeable membranes are always individualistic. Each kind has its own behavior, no two

kinds acting exactly alike. It would not be possible to accept without modification any theory which assumes that differential septa are alike in behavior. I do not mean to say that water is not simplified in structure as it is warmed, nor that such a change would not increase the rate of absorption, but it seems entirely possible to account for the high temperature coefficients found in absorption phenomena without the necessity of assuming such a change, or making it the sole change involved in the process. The substances of which the seeds are composed, membranes, embryo, and storage products, are all largely colloidal. These colloidal materials undoubtedly are modified in state of aggregation by being subjected during wetting to low or high temperatures. Higher temperatures usually increase dispersion and increase the water-holding capacity of organic colloids, and lower temperatures reverse the process. It does not seem possible that such changes could be absent during absorption, and they must go far to explain the differences in intake rates and the values of Q_{10}, which stand between those found for purely physical and purely chemical processes. Absorption is a complex process, probably involving both physical and chemical factors, and the values of Q_{10} may be considered the resultant of the effects of temperature on both classes of factors. The fact that we get about the same value for Q_{10} in absorption without a semipermeable coat as with such a coat indicates that the membrane is not necessarily the rate determining factor.

DENNY (2) has shown that membranes differ greatly in their power to transmit water. If the seed coat transmits water more slowly than seed substance can absorb it, the transmission rate is a limiting factor on the absorption rate. If the transmission power of the coat exceeds the absorption power of the seed substance, however, the latter determines the rate. Again, if seed coat, embryo, and endosperm form a very non-homogeneous structure, the absorption rate may be dominated first by one of the structures, and later by the others in succession, giving peculiar absorption curves, difficult to analyze mathematically.

It was noted that *Xanthium* seeds showed a very rapid initial intake during a minute or less, after which the rate broke sharply to a

lower rate. Two explanations suggest themselves for this. The coat may absorb water more readily than seed substance, and the initial intake may represent the saturation of the seed coat, or the rapid initial intake may be caused by the fact that at first the absorbing substance and water are in direct contact, but after a short time the water absorbed by the interior of the seed must penetrate a layer of saturated substance before it can reach the actively absorbing material. This outer saturated layer may offer resistance to intake in the form of friction with the moving water. As this layer becomes thicker and thicker all the time, it may tend more and more to reduce the absorption rate. Changes in the velocity of absorption due to such causes might be found in any case of water intake.

Finally, something should be said about the rise in the intake rate in split peas after a certain critical percentage of intake has been reached. During absorption one can observe that the hemispherical cotyledons become swollen first around the thin edge where water is penetrating from both sides. Looking at the flat side of the cotyledon, one can see that the edge has become raised up, while the center remains as it was originally, and appears depressed. The flat side has become concave. It seems evident that a band of dry material extends across the middle of the cotyledon from the center of the spherical side to the center of the flat side, and that imbibition forces at work in the edge of the seed are pulling at this dry band. After the critical intake has been reached, the center of the flat side soon swells out, and the concavity disappears. It is practically certain that the seed substance actually cracks apart during this process, leaving interior cavities that fill up with water. This idea is strongly supported by unpublished data, collected by DUDLEY J. PRATT, who worked in the laboratory of the University of Kansas, on the effects of acids and bases on the swelling of pea cotyledons. He was able to detect clearly the formation of such cavities during absorption, and some of them are of considerable size, as when strong hydrates or acids cause excessive swelling. This breaking up of the internal tissues of the cotyledon satisfactorily accounts for the peculiarities observed in absorption curves in split peas.

It is my conviction, after a number of years of experience with absorption phenomena, that absorption is a complex process dependent on a number of factors, some of which may be external, but many of which are internal. I have become convinced that we should not expect a single formula or rate law to apply to absorption in general. Each case of absorption is likely to present a problem in itself, and to differ, slightly at least, from any other case, because of both qualitative and quantitative differences in the numerous factors determining absorption rates.

Summary

1. This paper deals with the quantitative influence of temperature on the velocity of moisture intake by certain seeds, chosen for the presence and absence of semipermeable coats. *Xanthium pennsylvanicum* Wallr. and commercial and garden peas were used, the latter with coats removed.

2. The curves of water intake were found to be complex, but can be represented by a logarithmic equation or series of equations of the form $y=a \log_{10}(bx+1)+c$.

3. The analysis of the data presented does not support the theory of BROWN and WORLEY that the velocity of intake is an exponential function of the temperature, but the velocity of intake at any given moment in the seeds studied is approximately an inverse exponential function of the amount of water previously absorbed.

4. The mean value of Q_{10} in *Xanthium* seeds was in one instance 1.55, in another 1.83, and in split peas of the Small Scotch Yellow variety 1.6.

5. These values do not indicate that absorption is conditioned by some single chemical change like simplification of water to hydrone as the temperature rises, but are believed to indicate that absorption at different temperatures involves both physical and chemical changes.

6. The main chemical changes with rise of temperature are believed to occur in the colloids of the seed, and semipermeability, as such, is thought not to be an important factor in determining the rate of water absorption.

7. The paper considers critically the methods and interpretation of the similar work of BROWN and WORLEY on *Hordeum* seeds.

UNIVERSITY OF KENTUCKY
LEXINGTON, KY.

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PETIOLAR GLANDS IN THE PLUM[1]

M. J. DORSEY AND FREEMAN WEISS

(WITH PLATES XX, XXI)

True functional glands are present in the plum in three positions: on the leaf serrations, on the leaf base, and on the petiole. In the peach, plum, and cherry, the petiolar glands have been given a place of considerable taxonomic importance. In the course of the fruit breeding work at the Minnesota Agricultural Experiment Station, excellent material became available for a study of the glands in the plum in certain hybrids and pure forms. Since certain questions regarding their variation and morphology appeared to be as yet open, the investigation reported herein was begun.

In a historical review of the taxonomic use of the petiolar glands in the stone fruits, GREGORY (3) showed that the earlier writers had ignored these structures; while later pomologists had made use of them in distinguishing major groups, as in the peach. Other writers, however, questioned the taxonomic value of glands, because of the variation observed in number, shape, and position. From an extensive study of the leading varieties of the peach, GREGORY concluded that on typical shoots the glands were constant, and that in many cases their shape could serve to separate groups of varieties. He arranged the better known peach varieties under three types of glands, reniform, globose, and indistinctive, but pointed out that mixed and transitional types occur.

HEDRICK and others (4) record the gland condition on the petiole and leaf serrations in the descriptions of the principal varieties of plums in New York. Similar data have been brought together for cherries (HEDRICK *et al.* 5) and peaches (HEDRICK *et al.* 6). In the latter work the statement is made that "no one familiar with any considerable number of varieties of peaches

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would attach very great importance to glands in a system of classification."

On the whole, the tendency of later writers has been to attach less significance to glands in classification than has been done by earlier writers. In technical fruit descriptions, or in systematic classifications, it is evident that the value of a character as a distinguishing feature between forms depends largely upon its constancy of expression. Consequently, a statistical analysis was undertaken with the object of determining the number and disposition of glands in certain species and hybrids available.

Material

Data were first collected in 1914 in the F_1 generation of crosses between Burbank (*Prunus triflora*) and Wolf (*P. americana*), and Abundance (*P. triflora*) and Wolf. The gland condition was subsequently (August 1916) obtained in an additional number of species and interspecific hybrids. Single trees in each case of as nearly uniform age and size as possible were selected, and 400 leaves, on all trees which bore this number, were taken at random from vigorous 1-year shoots. By following this method of collection consistently on trees under fairly uniform growth conditions, the data obtained for the different forms are as nearly comparable as can be obtained under field culture.

There are a number of factors which influence gland development. In general it may be stated that those conditions which produce vigorous vegetative growth favor gland development, since on old trees or on trees subjected to unfavorable growth conditions, the petiolar glands become much reduced, sometimes even disappearing, although normally present in the varieties. On the other hand, position has an influence on glandular development. Leaves borne at the basal position on terminal growth, on fruit spurs or thorns and also in flower buds, typically bear no glands at all or have them less well developed than leaves borne at other points.

The arrangement of the glands (that is, whether opposite or alternate on the petiole or leaf) was not recorded. Glands occur both in pairs and alternately, near together or widely separated,

but since they vary independently on either side of the petiole, their relative position appears to be only incidental.

Variation in gland position and number

In horticultural literature, glands have been described with respect to color, type or shape, size, number, and position. In

TABLE I

SELECTED INSTANCES ILLUSTRATING METHOD OF RECORDING DATA AND SHOWING VARIABILITY OF GLANDS (A) ON DIFFERENT LEAVES WITHIN A VARIETY, (B) WITH REFERENCE TO POSITION ON PETIOLE OR LEAF BASE, (C) WITH REFERENCE TO DIFFERENT VARIETIES, AND (D) WITHIN SAME VARIETY DURING DIFFERENT SEASONS.

No. borne on		Abundance×Wolf no. 35		Burbank		Burbank×Wolf no. 9	
Petiole	Leaf	1914	1917	1914	1917	1914	1917
0	0	15	38	10	45	44	52
0	1	27	35	16	63	25	44
0	2	28	37	32	45	28	45
0	3	.....	1	.....	.....	.....	.....
1	0	34	40	6	8	25	33
1	1	29	33	8	29	63	48
1	2	1	16	9	25	9	6
1	3	.....	.....	.....	1	.....	.....
2	0	219	188	67	65	141	161
2	1	39	10	45	47	49	5
2	2	4	.....	33	18	1	1
2	3	.....	.....	.....	1	.....	.....
3	0	11	2	55	20	8	4
3	1	3	.....	33	17	6	.....
3	2	.....	.....	12	.....	.....	.....
4	0	.....	.....	33	7	.....	.....
4	1	1	.....	24	3	1	1
4	2	.....	.....	9	1	.....	.....
5	0	.....	.....	2	2	.....	.....
5	1	.....	.....	3	1	.....	.....
5	2	.....	.....	1	1	.....	.....
5	3	.....	.....	.....	1	.....	.....
6	0	.....	.....	2	.....	.....	.....
Glands on petiole		604	491	919	505	525	437
Glands on leaf		143	187	321	349	220	202

the plum the globose form is the prevailing type, and the true reniform type is found so seldom that little attention has been given to shape. The color of the mature glands in the plum is dark brown; and since these studies of number and position were made on mature leaves, color characters were also not recorded.

Data taken as to position and number were arranged in the form illustrated in table I, in which each leaf is classified with respect to the position and number of its glands. For instance, in Burbank 67 leaves bore two glands on the petiole and none on the leaf in 1914, and in 1917, 65 leaves fell in this class. A number of other varieties could have been included, but these were selected as typical of the great variability encountered.

Table I shows that in number and position glands are extremely variable on different leaves within a variety, but that the range of variability is fairly typical for each variety. The number of glands borne on the petiole is greater than the number borne on the leaf base, and while the number borne in each position is considerably different from season to season, yet the grouping opposite each class is quite similar in each variety in spite of the fact that the 1917 data were taken from different trees, but of the same clones, from those of 1914. Taking Burbank again as an illustration of variability, it will be seen that some leaves have no glands on either the petiole or leaf, while others bear as many as five on the petiole and three on the leaf. If observations as to gland condition made on a few leaves or herbarium specimens are considered from the standpoint of the variation shown, it will be evident that some caution must be exercised in classifying the gland condition.

Referring to the variability of glands within the species, it will be seen that a similar condition is found to that shown within varieties. A summary of the position and number of glands in all the species investigated is presented in table II, in which the gland condition is given for a total of 3477 leaves.

Four points are of interest in table II: (1) without exception there are more glands borne on the petiole than on the leaf base; (2) when there is one gland present it may be borne either on the leaf base or on the petiole; (3) when two glands are present, the larger number is without exception borne on the petiole; and (4) when more than two glands are present, without exception a strikingly larger number occur on the petiole.

For the convenience of the reader the data presented in table II, with the addition of data from certain interspecific hybrids,

TABLE II

SUMMARY OF DATA AS TO DISPOSITION OF GLANDS IN ALL FORMS UNDER INVESTIGATION SHOWING RESPECTIVE GLAND NUMBER BORNE ON LEAF BASE AND THE PETIOLE IN EACH SPECIES

GLAND NUMBER	P. AMERICANA (WILD); 877 LEAVES STUDIED		P. AMERICANA MOLLIS (WOLF); 400 LEAVES STUDIED		P. BESSEYI; 400 LEAVES STUDIED		P. CERASUS; 400 LEAVES STUDIED		P. DOMESTICA (SHIPPERS' PRIDE); 400 LEAVES STUDIED		P. PENNSYLVANICA; 400 LEAVES STUDIED		P. SIMONI; 200 LEAVES STUDIED		P. TRIFLORA (BURBANK); 400 LEAVES STUDIED	
	Glands on petiole	Glands on leaf	Glands on petiole	Glands on leaf	Glands on petiole	Glands on leaf	Glands on petiole	Glands on leaf	Glands on petiole	Glands on leaf	Glands on petiole	Glands on leaf	Glands on petiole	Glands on leaf	Glands on petiole	Glands on leaf
0	624	703	57	364	126	330	48	242	376	210	75	393	17	183	52	167
1	128	136	81	33	78	33	55	75	13	95	120	6	25	5	32	134
2	122	38	260	3	196	37	245	82	11	93	185	1	107	9	148	98
3	3	.....	2	.....	.....	.....	48	1	.....	2	16	.....	17	2	98	1
4	.....	.....	.....	.....	.....	.....	2	.....	.....	.....	4	.....	26	1	60	.....
5	.....	.....	.....	.....	.....	.....	2	.....	.....	.....	.....	.....	5	.....	9	.....
6	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	2	.....	1	.....
7	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	1	.....	.....	.....

are rearranged in table III, to emphasize the modal class for gland number on the petiole and on the leaf base. It will be seen in all the combinations summarized therein that the mode for gland number on the petiole (with only three exceptions) is two, and that on the leaf base it is zero. In other words, the 2-0 condition shown in figs. 1 and 11 is typical in the plum. Thus it appears that the glands in the plum are too variable, both in position and number, for accurate statements concerning their disposition on

TABLE III

SUMMARY OF GLAND CONDITION IN ALL FORMS STUDIED, SHOWING MODAL CLASS OF GLANDS BORNE ON PETIOLE AND LEAF BASE.

SPECIES OR CROSS	NUMBER OF TREES INCLUDED IN SUMMARY	TOTAL LEAF NUMBER	GLANDS BORNE ON PETIOLE			GLANDS BORNE ON LEAF		
			Number	Mode	Mean	Number	Mode	Mean
Abundance (*P. triflora*)	1	400	409	2	1.023	189	0	0.473
Burbank (*P. triflora*)	1	400	913	2	2.285	333	0	0.833
Wolf (*P. americana mollis*)	1	400	607	2	1.518	39	0	0.010
Abundance×Wolf crosses	38	15200	21956	2	1.440	9125	0	0.600
Burbank×Wolf crosses	22	8000	10406	2	1.300	5028	0	0.628
P. americana	3	877	356	0	0.406	212	0	0.242
P. Besseyi (Sand cherry)	1	400	407	2	1.018	107	0	0.268
P. Besseyi crosses	6	800	3359	2	1.866	788	0	0 438
P. Besseyi×*P. hortulana mineri* (Compass)	1	400	428	2	1.070	212	0	0.530
Compass crosses	8	1437	2019	2	1.405	514	0	0.357
P. cerasus	1	400	707	2	1.768	242	0	0.605
P. domestica (Shippers' pride)	1	400	35	0	0.088	287	0	0.718
P. domestica×*P. americana*	1	200	89	0	0.455	112	0	0.560
P. pennsylvanica	1	400	554	2	1.385	8	0	0.020
P. Simoni	1	200	438	2	2.019	33	0	0.165

any other basis than that of a statistical analysis. Other characteristics of glands, however, may be of distinctive value, and gland disposition may be sufficiently different and characteristic for a variety or species to be of taxonomic value. The outstanding feature of the data on the disposition of glands is that the mode for gland number on the petiole, with three exceptions, falls on two, and that the mode for the number borne on the leaf base in every instance is zero. This condition obtains notwithstanding the great diversity in the forms under investigation, and even in the three exceptions to a modal class of two on the petiole, the mode

was zero. This is significant in view of the fact that these three forms, *P. americana*, *P. domestica* (Shippers' pride), and *P. domestica*×*P. americana*, showed the greatest suppression of the glands of any of the forms included in this investigation. This condition will be given even greater emphasis in view of the connection found to exist between glands and the vascular system of the leaf.

Connection of petiolar glands with vascular system

With the status of the glands as to number and position shown by the statistical analysis in mind, it now remains to be seen whether or not there is a basic cause for the predominance of the 2-0 frequency.

The leaf trace in the plum has three bundles of conducting tissue at its departure from the vascular cylinder of the stem, which cause three gaps in the woody cylinder. The central bundle extends up the petiole, through the blade, and branches successively at the large lateral veins. The outer bundles give rise to strands which run along the upper side of the petiole, forming pronounced ridges on either side. These strands run directly to the petiolar glands, or to the large ones borne on the leaf base, and terminate there. The term petiolar gland, therefore, will be used in this connection to include both. The lateral strands are shown in fig. 30, which was drawn from a young leaf, and they are equally conspicuous whether the glands are borne on the leaf base or some distance down on the petiole. Where there is more than one gland on either side of the petiole, branches from the lateral strands connect with them.

On the other hand, the glands of the leaf serrations have a distinctly different vascular connection. Instead of being connected by branches with the lateral strands, glands in this position have their vascular connections with the central bundle through the lateral veins. It appears, therefore, that on the basis of differences in their vascular connections the petiolar glands and the glands borne on the serrations can be placed in two distinct classes. Other considerations also support this view. The petiolar glands are much larger than those on the serrations and may show differences in shape, such as the reniform or necked types,

which would readily differentiate them. Also under orchard conditions the glands on the petiole may be active much later in the season. That there is no relation between the glands in the two positions is further shown by the fact that in some species, as in *P. americana*, glands are typically absent on the serrations but present on the petiole or leaf base.

Glands which could not readily be classified as belonging to either the leaf serrations or the petiole were not numerous, consequently error from this cause has not entered to any appreciable extent into the statistical classification. There was also little difficulty in determining whether glands were borne on the petiole or leaf base, since in most cases there was no leaf tissue between the glands and the base of the blade. When leaf tissue was so present they were classed as being borne on the leaf base.

The question now arises as to whether the structure of glands on the petiole is similar to that on the leaf base. GREGORY (3) showed that glands borne on the petiole and leaf base in the peach were true glands, the upper part being composed of long rectangular cells rich in cytoplasm, and with large nuclei, while the central part is made up of parenchyma cells characteristic of glandular tissue, into which extend ramifications of conductive tissue. The structure of the glands in the plum borne on both the petiole and serrations has been examined on leaves just emerging from the bud, and on mature leaves with vigorous active glands, and is found to be similar to that reported by GREGORY in the peach.

The similarity in structure between the glands borne on the petiole and on the serrations led GREGORY to suggest that the former arose from the latter. Such an origin would imply that both are of the same rank, and that the tissue of the leaf blade is more or less indeterminate with that of the petiole, and would be in accord with the condition of the petiolar glands in some species of willow, notably *Salix lucida* (fig. 10), in which the glands are minute, numerous, and crowded together at the leaf base, suggesting a proliferation of leaf tissue along the petiole.

From these considerations it appears that there is justification for regarding the glands of the petiole, and the larger ones borne

on the leaf base, as of the same structure but of different rank from those borne on the serrations. This is in keeping with the evidence presented in the statistical analysis in which the number two figured so prominently, that is, two glands on the petiole and none on the leaf base, or one in either position, or less frequently, two on the leaf base. The points emphasized are of significance from the standpoint of phylogeny, and will be given greater emphasis from that standpoint.

Phylogeny of leaf as indicated by glands, vascular system, stipules, and abscission layers

There are structures other than the glands whch are significant from the standpoint of the ancestral type of leaf in *Prunus* and related genera. COOK (1) called attention to a joint in the leaves of Amygdalaceae "just above the insertion of the stipules," and states that the "basal section of the leaf below the joint" has a separate abscission from that of the leaf proper. This "basal section" is regarded as belonging to the leaf on the basis of the attachment of the stipules to it, although the stipules themselves absciss early, and hence "the persistence of the base of the leaf" has been overlooked. GOEBEL (2) characterizes stipules as "appendages arising at the insertion of a leaf, attached either wholly to the petiole or to the stem, or to both." SINNOTT and BAILEY (12) regard the stipules as arising through the stimulus of the growth of the lateral leaf trace, and although they are morphologically integral parts of the leaf, in some exstipulate families having trilacunar nodes, they are represented by mere swellings opposite the leaf trace. In some stipulate genera with opposite leaves, as *Viburnum*, the stipules arise midway between the insertion of the petioles, apparently directly from the stem. COOK also states that in Texas this basal section in the peach may remain alive for a year or two and then wither away; while in Maryland it lives through the winter and separates in the spring, leaving a fresh green scar.

In most of the plums studied in this investigation, this structure does not separate at all, but may be clearly observed (the petiole scar with its three bundle scars, and the two stipule scars at its

sides) on 3-year or even 4-year-old wood. Some vestige of it often remains a year or two longer, but usually after this time it begins to slough off.

It was not until some young trees of *Amygdalus Davidiana*, which were making an extremely rapid spring growth, were examined that the separation which COOK described was found. Ordinarily it requires some effort to remove the dry scalelike remnant left after the fall of the leaf, and usually there is more or less tearing of the bark; but in the case of *Amygdalus Davidiana* this structure separated easily and clearly when started with a knife point. In many cases after the rapid spring growth it cracked and separated without any outside stimulus, and later a large proportion fell as a result of further enlargement at the node. The condition is represented in fig. 5, which shows the separating scale, and fig. 31, which shows its structure in greater detail.

Examination of rapidly growing shoots of other *Prunus* species showed that a similar separation may take place, especially in some of the *P. Besseyi*×*P. triflora* hybrids, although in no case quite so sharply as in *Amygdalus*. At least a partial explanation of the fact that the separation of the scar scale occurs in some species of *Prunus* and not in others, can be made on the basis of the character of the swelling of the node below the leaf insertion. When it is straight in outline, it makes an acute angle with the line of the shoot and terminates in the leaf scar along a narrow ridge, as in *Amygdalus* (fig. 5). The rapid growth in spring of tissue underneath forces off the dead scale at the apex. If, however, the node is swollen, with a rounded profile, and the leaf scar is well buttressed below, as in the extreme type shown in fig. 4, the scale does not separate, and cannot be removed without tearing the bark. In either case, whether separation is immediate or delayed, it is only the shedding of dead tissue, just as bark is shed, and is done without the aid of a definite abscission zone (LOYD 9), and consequently is not true abscission.

A search for corroborative evidence as to the nature of this structure showed that in a number of genera it is not uncommon for clean cut separation of a scar scale to occur when rapid growth

begins. Some of the species which show the separation of the old leaf scar more clearly even than *Amygdalus* are *Shepherdia argentea*, *Cornus stolonifera*, *Tilia americana*, *Rhamnus cathartica*, and *Celtis occidentalis*, the first two of which are illustrated in figs. 16 and 17. All of these have simple leaves and lack petiolar glands, and *Cornus* and *Shepherdia* are exstipulate and have entire leaves, which, according to SINNOTT and BAILEY (**11, 12**), is an advanced state of node and leaf morphology. Hence we must regard the structure to which the stipules and petiole in *Prunus* are articulated, not as an additional foliar element, but as an outgrowth from the stem; and therefore abscission of this kind does not necessarily indicate an additional foliar element.

The manner of insertion and abscission of the stipules in the plum furnishes additional evidence that the structure described by COOK as a persistent leaf base is in reality a part of the stem, and that the leaves of Amygdalaceae cannot therefore be jointed.

In some Rosaceous genera, as *Potentilla* and *Rosa*, the stipules are adnate to the petiole, forming a somewhat sheathing base, and fall with the leaf. In others, as *Pyrus* and *Prunus*, the stipules are separate, or nearly separate, from the petiole, and abscis soon after the buds unfold. In *Prunus* the stipules usually drop long before the leaf, but occasionally they persist throughout the growing season, and even over winter, in vigorous, late growing branches in which cold weather has stopped further growth. The point of normal abscission is illustrated in fig. 32 (*P. hortulana mineri*). The stipules, like the petiole, separate at a definite abscission layer at their base (figs. 1, 2). As COOK pointed out, the joint of the latter lies above the stipules, that is, distally to them, although since the abscission lines of the petiole and the stipules form a sort of crescent with the points upward, a face view of the stem shows the stipule scars above that of the petiole (figs. 31, 32).

The typical leaves of many stipulate genera of the Rosaceae have stipules adnate to the petiole, forming a more or less sheathing base. This condition is also to be found in the bud scales and the scales transitional to leaves in *Prunus*. Morphologists regard bud scales as relatively primitive in structure, since they have not specialized to serve such varied functions as the leaves themselves.

Accordingly, the bud scales of *Prunus* may be taken as an index of the ancestral leaf type. A series of bud scales and scale leaves grading into true leaves is shown in figs. 18–29, which were taken from a young shoot of the Compass cherry (*P. Besseyi*×*P. hortulana mineri*).

It may clearly be seen that in the outer scales the stipules are represented by blunt lobes, as large as the central lobe which represents the leaf blade. The inner scales show progressive reduction in size of the lateral lobes and increase of the middle one, accompanied by differentiation into stipules and lamina. It will be noted, also, that there is progressive splitting of the stipules from the petiole. In the mature leaf of the plum this splitting has progressed to the base of the petiole, so that leaf and stipules have separate abscission, but from one originally continuous abscission layer. *Prunus avium*, as represented by the Dyehouse cherry, is at a somewhat intermediate stage. In the leaves near the base of a shoot, the stipules are clearly adherent to the petiole, while in the upper leaves they are separate, as in the plum. In all these transitional bud scales separation from the axis is clearly below the stipules, and there is no evidence of an abscission layer above them cutting off the middle lobe or leaf blade (fig. 2); hence the stipules in the plum must be regarded morphologically as integral with the leaf base, although the course of development separates them from the petiole in the mature leaf.

It remains to interpret the structure of the petiolar glands in relation to a more primitive type of leaf. Their organization and their occasional proliferation into leaflike outgrowths indicate that they are reduced structures. This change from a glandular to a foliar structure was noted by Cook (1), who described the occurrence of "small oblong or spatulate leafy organs on the upper part of the petiole, taking the place of the nectaries" in certain varieties of apricots. A similar transformation has been observed in *Crataegus*, as well as a number of species of *Prunus*, and in some of the apricot hybrids at the Minnesota Experiment Station it is of almost regular occurrence on vigorous shoots of young trees. Some of the variations in this transformation are illustrated in figs. 11–15. The view that the leaves of the Amygdalaceae are

jointed, led COOK to conclude that the ancestral leaf type of this group was compound, the nectaries representing "rudiments of divisions of compound leaves." It should be pointed out, however, that if the modern plum leaf represents the terminal leaflet of an originally compound leaf, the glands, representing reduced lateral leaflets, should be found below the joint by which the terminal leaflet is articulated to the rachis. It is obvious that being situated on the petiole above the joint, they cannot represent lateral leaflets of an ancestral pinnate form. Microscopic sections of the petiole at the leaf base do not show an abscission layer subtending the blade, and the presence of one is not indicated by the normal manner of shedding the leaves. It may be safely concluded, therefore, that the leaf blade of the plum is not articulated to the petiole, as in *Citrus*, *Berberis*, or *Trifolium*. Sometimes, however, if there has been late growth in the fall and the leaves are immature when the first frosts occur, the leaf axis may be broken anywhere from the middle of the blade to the base of the petiole, although most frequently at the juncture of the blade and petiole. In this case the twig enters the winter with a part or all of the petiole adhering at each node, which, however, usually breaks off at the point of normal abscission by spring.

Glands, however, may represent divisions of an alternate divided or pinnatifid leaf, such as *Fragaria*, *Potentilla*, and other genera of the Rosaceae possess. The frequency of the occurrence of two glands suggests a ternate leaf such as that of *Fragaria*. The presence of additional glands may be accounted for on the basis of branching of the lateral bundles, or by the common transition from ternate to quinquefoliate or pinnate leaves (LEWIS **7, 8**). Some pinnate-leaved forms of *Potentilla* show reduction of the lower divisions to smaller structures than are the leafy outgrowths in the position of glands in the apricot. Furthermore, the lower divisions are frequently alternate instead of paired, as is also the case with the petiolar glands in *Prunus*.

It will be recalled that in the plum the two lateral bundles which connect with the glands terminate there, and do not contribute extensively to the vascular system of the blade. In ternate leaves which have three strands, the outer two provide the

vascular system of the lateral leaflets, and this is also frequently the case when there are numerous lateral leaflets, as in pinnate forms of *Potentilla*.

On foliar evidence the connection of the stone fruits, whether regarded as a tribe of the Rosaceae or as a separate family, with the Potentilleae is quite direct. The nodal anatomy is the same (SINNOTT and BAILEY **12**) and the steps in leaf evolution appear to be: (1) reduction of the lateral leaflets of a ternate or pinnate-divided leaf to petiolar glands; and (2) splitting of persistent adnate stipules from the petiole. In this series *Prunus avium*, with an extensive development of glands, both in number and size, or the apricot with a frequent reversion to leafy structures in place of glands, would stand below *Prunus americana* with its almost glandless petioles. GREGORY (**3**) regarded the globose gland as more primitive than the reniform, since when normally glandless leaves produced glands, they were always of a globose type. If, however, the trend is toward reduction of glands, the glandless petiole would be the highest type, and the globose condition transitional between it and the reniform.

It has been customary to trace the connection of the drupes with the more primitive Rosaceae through *Spiraea* (RYDBERG **10**). Considered on the basis of floral evidence alone, this seems a logical sequence, *Spiraea* being intermediate in form of receptacle and number of carpels between *Potentilla* and *Prunus*. SINNOTT and BAILEY (**12**) have shown, however, that *Spiraea* is exstipulate and possesses a unilacunar node, while all species of *Prunus* have stipules and a trilacunar node. It would appear that forms with stipules could not be derived from forms which lack them. The relationship of the stone fruits to the true Rosaceae is probably more direct, and on the basis of anatomy there is less reason for separating them as a distinct family than for considering them a well defined and specialized tribe.

Summary

Examination of over 30,000 leaves belonging to 15 species and interspecific hybrids of the plum shows that two glands typically occur on the petiole, or less frequently on the leaf base.

On the basis of vascular connections the glands on the petiole or leaf base are of a different order of structure from those on the leaf serrations.

The stipules in the plum are morphologically integral with the leaf base, and separate from the stem by a common abscission layer. A portion of the node bearing the leaf and stipule scars is subsequently shed in some species of *Prunus* as in other woody genera; but the portion thus shed is not an additional foliar element.

On the basis of nodal anatomy and the presence of reduced structures, the ancestral type of leaf in the plum is considered to be a ternate lobed or divided simple leaf, the petiole glands representing the suppressed lateral members. In floral structure and nodal anatomy *Prunus* and related genera form a logical series with the Potentilleae, and should be considered as a specialized tribe of the Rosaceae.

AGRICULTURAL EXPERIMENT STATION
UNIVERSITY OF MINNESOTA

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EXPLANATION OF PLATES XX, XXI

PLATE XX

FIG. 1.—Section through node showing abscission zone by means of which the leaf is shed; *a*, only abscission zone present.

FIG. 2.—Showing continuous abscission zone (*a*) for stipule and petiole at early stage of growth.

FIG. 3.—Dark line at base of stipule showing point of abscission; note that it is distal to attachment of petiole.

FIG. 4.—Instance of extreme swelling in node below point of abscission of leaf; in such instances scar scale is not shed.

FIG. 5.—Enlarged view of shedding of scar-scale (*a*) in *Amygdalus Davidiana* as result of early spring growth; shedding of this type occurs only when contour of node is relatively flat.

FIGS. 6–9.—Variation in gland position and number; types illustrated are 2-0 (2 on petiole and 0 on leaf base), 1-0, 1-1, and 0-1.

PLATE XXI

FIG. 10.—Leaf of *Salix lucida* showing glands similar to those of leaf serrations crowded at base.

FIGS. 11–15.—Types of proliferation of petiolar glands into leafy outgrowths.

FIG. 16.—Node of *Shepherdia argentea* showing shedding of scar-scale similar to *Amygdalus*.

FIG. 17.—A node of *Cornus stolonifera* showing same as 16.

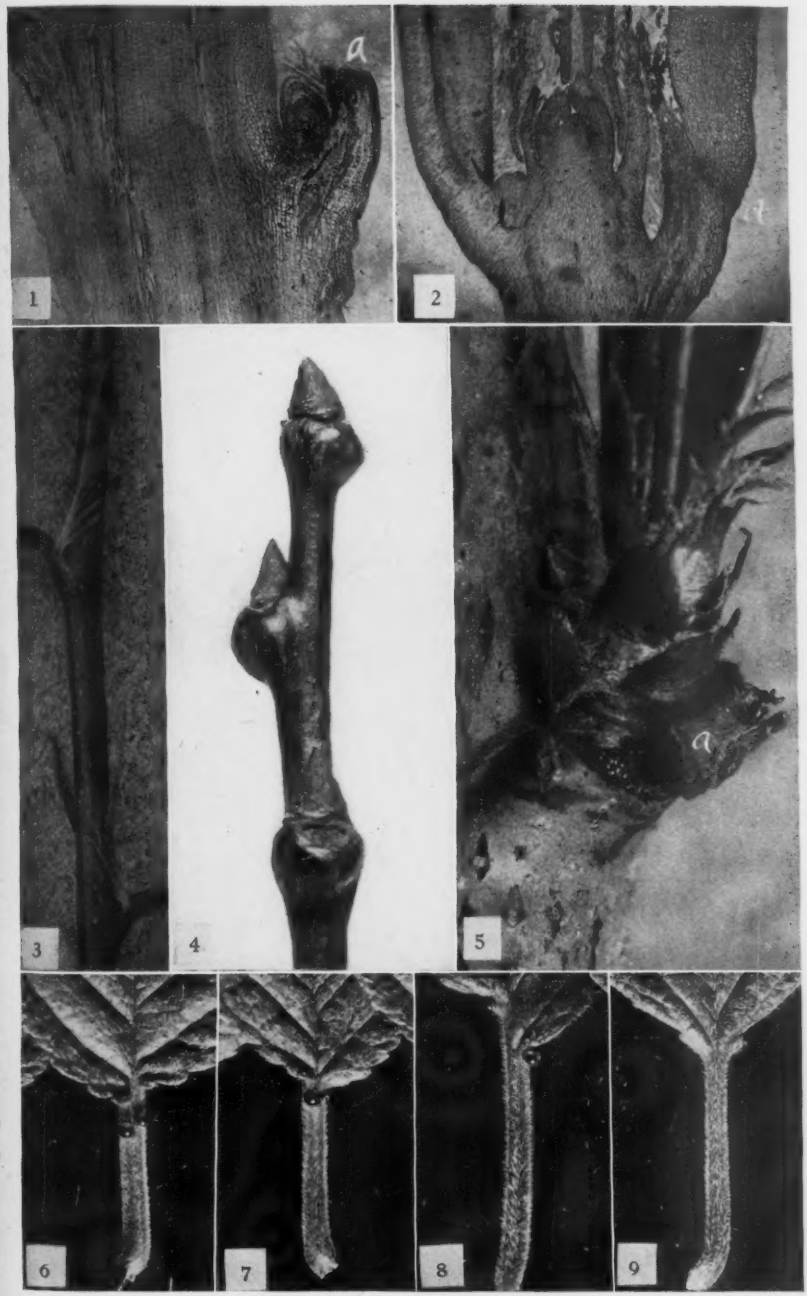
FIGS. 18–28.—Bud scales and basal leaves from young shoot of Dyehouse cherry, presenting series in separation of stipules from leaf blade.

FIG. 29.—Enlarged basal leaf illustrating venation of stipules and leaf blade; note that veins of stipules arise as branches of lateral strands.

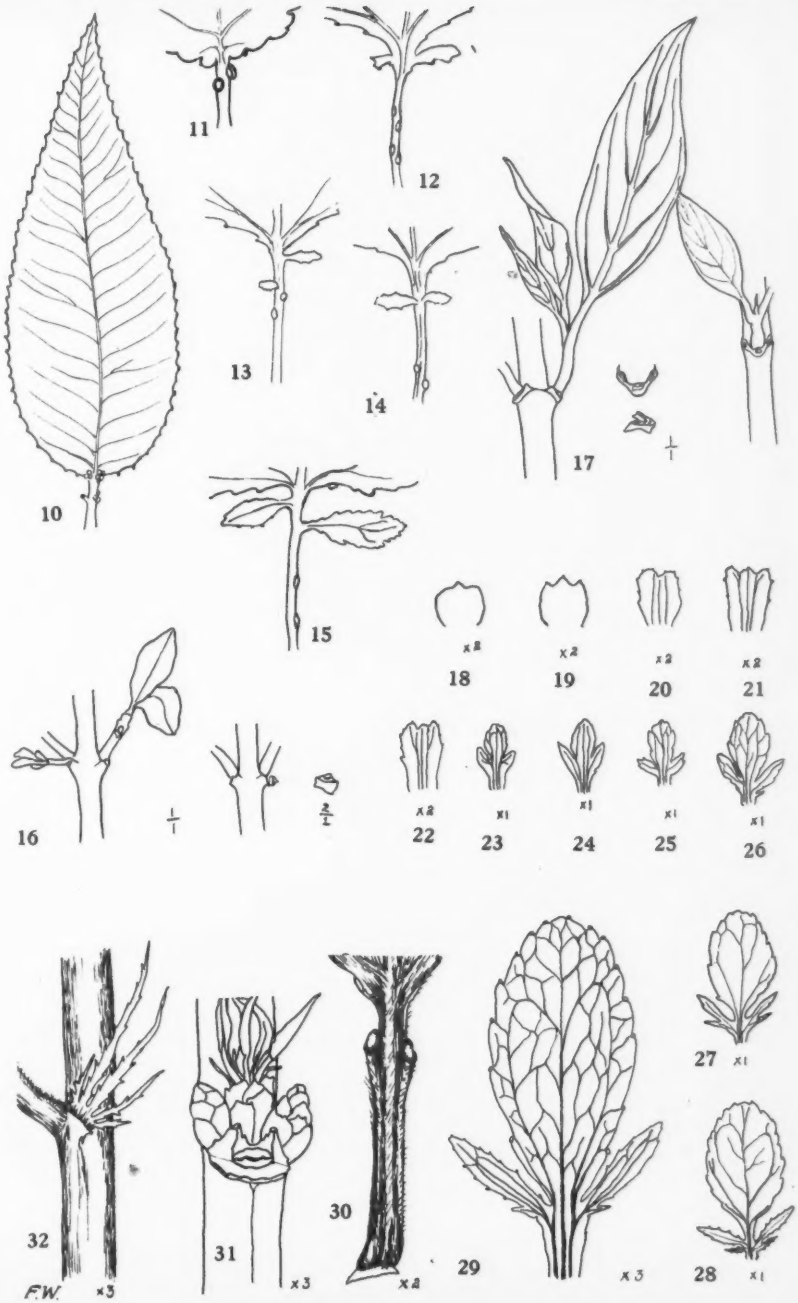
FIG. 30.—Petiole showing prominence of lateral bundles in young leaf.

FIG. 31.—Shedding of dead scar scale in *Amygdalus Davidiana* from which stipules and petiole abscissed previous season.

FIG. 32.—Node of young plum stem showing relation of line of abscission in stipule and petiole.



DORSEY & WEISS on GLANDS



DORSEY & WEISS on GLANDS

INHERITANCE OF ALEURONE COLOR IN MAIZE

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 265

MERLE C. COULTER

Interested in the pedagogical value of plant genetics, the writer was impressed with the fact that the bulk of our knowledge comes from experiments with corn. An investigation was undertaken, therefore, with no more definite object than to discover how dependable some of these classic experiments actually are. During three years of rather interrupted and limited investigation, this undertaking, as might be expected, has been rewarded by numerous results that have been interesting and suggestive, but by practically none that as yet can be regarded as conclusive. In view, however, of the number of investigators, professional and amateur, who are now interested in inheritance in corn, it is felt that a brief statement of a few of the results may be useful.

Technique

The writer's experiences in matters of manual technique will undoubtedly be of interest to amateurs. The grosser mechanics of corn crossing are simple and familiar. The difficulties are mainly two: (1) to avoid exposing the silks to chance foreign pollen at the time the cross is made, and (2) to insure full pollination, and hence full ears. It is common practice to remove, totally or partially, the bag which covers the silks when the pollen is applied. This involves momentary exposure of the silks to chance foreign pollen, plenty of which is almost sure to be circulating in the air. Thorough distribution of the applied pollen over the silks is then attempted by shaking the bag in some way. In the hands of an experienced operator this method is not only adequate but rapid. When the writer attempted this, however, the results were not satisfactory. Less than half the ears were fully pollinated, and there were quite a number of cases in which about 5 or 6 grains of foreign pollen had evidently been admitted. For the second season's work, therefore, a simple mechanical device was employed,

and this effectually solved the difficulties. This is a so-called corn-pollinator, a description of which has already been published.[1] Even in inexperienced hands this method will not only insure full pollination, but will never admit foreign pollen. Its drawback lies in the fact that it lengthens the process somewhat; hence it is felt that this device may be recommended to all save experienced operators, who are conducting extensive experiments.

Normal ratios

An attempt was made to discover how exactly certain complex ratios might be predicted. Material was sought in which a number of factors could interact to produce various but predictable (?) ratios. Nothing was more suitable than the set of factors involved in the inheritance of aleurone color in corn. These factors have already assumed an important rôle in pedagogy. R and C are complementary factors, the presence of both being required for the production of red aleurone, and P[2] is a supplementary factor which changes red to purple (PRC is purple, pRC red, PrC white). Other factors have been added to this set by EAST and EMERSON, but they are not dealt with in this paper. The original stock material was furnished by EAST, to whom the writer wishes to express his appreciation.

Leaving out of consideration those well established cases in which a 1:0 or 3:1 ratio is produced, it was found that the material, as originally provided, could be manipulated to produce 8 different ratios. Appropriate crosses were made, therefore, and of the resulting crop all ears containing 64 or more grains are considered in the following summary.

I.—0:1:1 (no purple:50 per cent red:50 per cent colorless) ratio predicted; from pprrCC×ppRrCC and reciprocal. Eight ears gave a total of 0 purple:559 red:659 white, or an average

[1] BOT. GAZ. **58**:63. 1919.

[2] EAST and HAYES use the symbol P for this factor, while EMERSON uses Pr for what is probably the same factor.

EAST, E. M., and HAYES, H. K., Inheritance in maize. Conn. Agric. Exp. Sta. Bull. no. 167. pp. 142. *pls. 25*. 1911.

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ratio of 0:0.92:1.08. The extreme ratios on individual ears were 0:0.81:1.19 and 0:1.03:0.97. Conclusion: slight but chronic excess of colorless grains.

II.—0:9:7 predicted; from ppRrCc selfed. Five ears gave 0:418:320, or an average ratio of 0:9.06:6.94. Extreme ratios on individual ears, 0:8.77:7.23 and 0:9.45:6.55. Conclusion: predictions fulfilled.

III.—0:3:5 predicted; from ppRrCc×pprrCc. Three ears gave 0:260:430, or an average ratio of 0:3.01:4.99. Extreme ratios on individual ears, 0:3.19:4.81 and 0:2.94:5.06. Conclusion: predictions fulfilled.

IV.—1:1:2 predicted; from pprrCC×PpRrCc. Only one ear with over 64 grains obtained.

V.—9:9:14 predicted; from ppRrCc×PpRrCc. Four ears gave 229:242:262, or an average ratio of 10.11:10.35:11.54. Extreme ratios on individual ears, 10.14:12.69:9.17 and 6.51:9.83:15.55. Conclusion: decided but not chronic excess of colored grains.

VI.—3:3:10 predicted; from ppRrCc×PprrCc and pprrCc× PpRrCc. Eight ears gave 252:235:765, or an average ratio of 3.22:3.00:9.78. Extreme ratios on individual ears, 3.60:2.07: 10.33 and 4.42:3.58:8.00. Conclusions: predictions fairly well fulfilled, considering smallness of population used.

VII.—9:3:20 predicted; from PprrCc×PpRrCc. Only one ear obtained with over 64 grains.

VIII.—27:9:28 predicted; from PpRrCc selfed. Thirteen ears gave 1534:464:1560, or an average ratio of 27.59:8.35:28.07. Extreme ratios from individual ears, 23.54:9.92:30.54 and 28.97:11.03:24.00. Conclusions: predictions well fulfilled; slight tendency toward excess of purple at expense of red (as was regularly the case except, strangely enough, in the two individual ears cited under extreme ratios) may well be accounted for by improper classification, throwing a few deep red grains with the purple.

From this preliminary experiment the general conclusion was drawn that ratios produced by the interaction of these three factors were sufficiently distinct to be readily recognized in the vast majority of cases. This was confirmed by later experience,

which included also several other types of ratios produced by these same factors. Actually the only difficult distinction which was encountered was between 9:9:14 and 3:3:2, for the former (V) commonly showed a deficiency of colorless grains. How persistent and significant this deficiency is I will not venture to conclude from the limited data. Elsewhere recognition was easy so long as P, R, and C were the only factors dealt with.

Dominance

The literature is likely to leave one with the impression that dominance is complete with this set of factors. Uncertain on this matter, the writer wondered whether there was any hope of distinguishing genotypes from superficial appearance. In other words, was a grain with the formula ppRRCC a very dark red, ppRrCC or ppRRCc a lighter red, and ppRrCc a still ligher red? That such a thing might be possible was suggested by the following observation. When individuals of the formula ppRRCC were selfed, they regularly produced ears on which all of the grains were not only red but the same intensity of red. Obviously the grains were all of the same (ppRRCC) genotype. Likewise, ppRrcc × pprrCC would produce ears on which only 50 per cent of the grains were red, but always the same intensity of red. Here, also, all the red grains would be of the same (ppRrCc) genotype. In contrast with this were ears so produced that the colored grains represented more than one genotype. It was common in such cases for quite a series of color intensities to appear. Whether these different intensities to any degree represented the different genotypes was an open question, but one that could be readily decided.

An ear was chosen which had been produced by ppRrCc × PpRrCc. This particular ear was noteworthy in two respects. In the first place, where it should have shown a 9:9:14 ratio it actually gave 57:61:57. In the second place, an unusual range of color intensities appeared. Now the 9 purples theoretically should have been distributed among the following genotypes: 1 PpRRCC : 2 PpRrCC : 2 PpRRCc : 4 PpRrCc; the 9 reds, 1 ppRRCC : 2 ppRrCC : 2 ppRRCc : 4 ppRrCc. The writer therefore classified the grains on the basis of color intensity, with some

hope that four intensities of each color could be recognized. This proved impossible, since the series of intensities was practically continuous. At this point, therefore, I was forced to conclude that at least genotypes could not be sharply separated on the basis of color intensity. There yet remained the possibility, however, that color intensity might to some degree depend on genotype, the boundaries of the classes merely being obscured by individual variation. With this in view the whole series of colored grains was arbitrarily divided into several intensity classes, and these classes were planted separately and selfed.

Class W, indicating colorless, gave six large ears, all of which, of course, showed 100 per cent colorless grains.

Class R indicated faint red. This was the minimum color intensity, and may best be described by saying that a casual glance would discover no color in such grains. More careful scrutiny, however, reveals an evenly distributed (not mottled or variegated) but very faint aleurone color. In the original count of the parent ear these grains had been classified as red. Only one ear was obtained from this class, but that was very striking. Most of its grains were colorless, but some were the same faint red as the parent, and absolutely none were of any deeper intensity. Viewed at a little distance, this ear would be said to contain 100 per cent white grains.

Class R′, indicating light red, produced two ears, on which the ratios were 0:42:31 and 0:88:54 respectively. Without hesitation these were both diagnosed as 0:9:7 ratios, indicating a ppRrCc genotype.

Class R″, indicating red, produced three ears, with respective ratios of 0:76:59, 0:176:63, and 0:24:8. One feels safe in calling the first a 0:9:7 and the last two 0:3:1 ratios. The conclusion from this is that ppRrCC or ppRRCc or both have a tendency to produce a more intense aleurone color than does ppRrCc. The question arises whether the appearance of one 0:9:7 ratio from the red class was due to improper delimitation of the classes in the first place, of which there was, of course, every possibility; or whether it might have been due to inevitable overlapping of the classes owing to individual variation. I am in no position to

answer this, since I cannot say whether the particular grain which gave the 0:9:7, although included in the red class, was noticeably lighter than the other two.

Class R‴ indicated dark red (or purple?). In the original count these grains had been included with the red, but the intensity of color was such that it demanded close scrutiny to distinguish them from the purple. Four ears came from this class. Of these, one gave 0:130:33, and the other three 0:200:0 (no exact count was made of large homogeneous ears). The first was evidently a 0:3:1, with an excess of red grains, while the others obviously represented the ppRRCC genotype, the conclusions suggested being similar to that of class R″.

Class P indicated faint purple, with the same significance as R for faint red. This class gave three ears, as follows:

Faint purple	Faint red	Colorless
5	4	21
53	36	141
51	14	141

No attempt is made at present to attach any significance to these counts. In fact, it is felt that such counts are rather untrustworthy, since the color is frequently so faint as to lie at the very limit of visibility. Sufficient at present that not so much as a single light purple or light red was produced on these ears; only the faint color of the parents was regularly produced.

Class P′ indicated light purple, and gave three ears, 142:47:52, 34:14:40, and 13:1:12. The first is probably a 9:3:4 and the others 27:9:28 ratios.

Class P″ indicated dark purple, and gave one ear, 79:34:85, probably a 27:9:28 ratio with an excess of red.

The general conclusion from the preceding is that genotypes may be distinguished, to a degree, on the basis of color intensity, at least among red grains. One rather familiar with the material should be able to pick out a given genotype in most cases, particularly if he discarded intermediates, which the writer did not.

Returning now to the faint grains, one is confronted by three possible explanations: (1) these are grains, properly colored, in which an inhibitor tends to lessen materially the intensity of the

color; (2) they are grains, properly colorless, in which there is some partial substitute for the R or C (probably the latter, referred to later) factors or both; (3) they represent something entirely unrelated to the set of factors under discussion. That the second is a likely explanation is suggested by three facts.

1. The count of the original parent ear showed a marked deficiency of colorless grains. The faint red and faint purple grains had, in that count, been classified as colored. If they were truly colorless grains the original ear would have very closely approximated the predicted 9:9:14 ratio.

2. The nature of the original cross was such that every grain must be Pp or pp, but never PP. Inbreeding, therefore, might give ears with some red and no purple grains, but could never give ears with some purple and no red grains. Actually that is what occurred. This is, of course, merely negative evidence. Positive confirmation, however, comes from a similar experiment conducted with slightly different material. An ear produced by PpRrCc selfed, which gave an ideal 27:9:28 ratio, was used as the basis of an experiment similar to the preceding. The general results were about the same and need not be discussed in full. Among the purple grains, however, several produced ears which showed purple and colorless, but no red grains, and one produced a full ear of purple grains alone. This is to be expected from the fact that genotypes including PP, although not present in the previous ear, are present here. Such being the case, the behavior of the faint purple grains from this ear should prove significant. From that class came the following four ears:

Light purple	Faint purple	Faint red	Colorless
0	Some	Some	Many
0	Some	Some	Many
0	Some	0	Many
1	34	0	4

These certainly suggest the presence of PP in the last two cases, while Pp may be inferred for all the others. It is very likely that the last ear represents the homozygous condition for faint purple, whatever that may be, the color being present but indistinguishable in 4 grains.

3. EAST and HAYES (*loc. cit.*) describe in certain of their families grains which they call particolored. Their description leaves little doubt that the writer is dealing with the same phenomenon. These authors carried their work far enough to assign the P(R)c formula to these grains.

The tentative conclusion, therefore, may be reached that particolored (faint) grains lack C but contain some partial substitute. Just how this substitute is inherited is not clear as yet, but the fact that it is heritable is undoubted. It is probable, although not certain, that the same relationship between P and R as occurs in the inheritance of the normal full color maintains itself also under the particolored system. It must also be noted that this unknown substitute for C is by no means always effective in bringing any distinguishable color; its powers of expression seem to be limited by conditions, a matter which will be discussed later.

The question is now raised whether, in view of the possibility of a complete series of color gradations, reliable counts of purple, red, and colorless phenotypes can always be made. In answer one may safely state that the phenotypes stand out sharply unless particolored grains appear; the gap between light red and colorless is a wide one. Particolored grains by no means appear in all cases; the condition which brings them may or may not be present in the germ plasm. When they do appear, they do so in considerable numbers, so that a glance at the ear as a whole will determine whether or not one has them to deal with. Thereby the investigator is warned to focus sharply upon the boundary between light colored and particolored, but even under the most practiced eye some slight error is likely to creep in at this point.

An anomalous case

The possibility of at least partial substitution for the C factor has been mentioned. We may be dealing with something of the same sort in the following unusual case. EAST provided the writer with an ear produced by PPRrcc×pprrCC. The expectations were obviously fulfilled, half of the grains being purple and the other half colorless. The former, in the many crosses made, regularly revealed the PpRrCc formula, which was expected; while

the latter, in all cases but one, revealed PprrCc. In this one case the individual produced by this supposed PprrCc grain was selfed, and gave a ratio of 46:0:36. This is a perfect 9:0:7 ratio, such as would be produced by PPRrCc, but such a formula is out of the question in view of the history behind the ear. The obvious but heterodox suggestion is that some unusual condition is present, which, together with both P and C, results in purple aleurone; while with C alone it gives, not red, but colorless.

That this is a pathological case is suggested by two facts: (1) practically all the grains on this ear had their pericarps split irregularly, an unusual condition; (2) when planted, they germinated very slowly (or not at all), giving 3-inch plants at the time that all the neighboring rows had attained 3 or 4 feet; by harvest time a few small tassels had just appeared, but no silks.

Mottling

EMERSON (*loc. cit.*) has described the following situation in certain of his families. When the R factor enters the cross with the male parent only, a mottled aleurone results, while in all other cases a solid aleurone color is produced. Thus, RRcc×rrCC gives 100 per cent solid red; rrCC×RRcc gives 100 per cent mottled red; RRCC×RRcc gives 100 per cent solid red; RrCC selfed gives 50 per cent solid red, 25 per cent mottled red, and 25 per cent colorless.

The writer wishes to express his appreciation to EMERSON for providing material of the well known C tester and R tester. These races behaved with considerable regularity, for crosses between them consistently yielded 100 per cent solid purple grains when R tester was used as the male parent (PPRRcc×PPrrCC), and 100 per cent mottled grains when C tester was used as the male parent (PPrrCC×PPRRcc).

Splashed purple grains, recognized by EAST (*loc. cit.*) in most, but not all, of his families, were doubtless due to the same phenomenon. In the particular material of EAST's which was furnished, however, nothing of the sort could be identified, even in the very numerous cases in which the R factor came in with the male parent only. It was felt, therefore, that crosses between the material from EMERSON

and that from EAST would prove interesting. Evidently the former contains something which the latter lacks, and this something brings mottling instead of solid color, provided always the R factor comes in with the male parent only. Such crosses should help interpret this mottling, and should also reveal whether the P, R, and C factors of these two investigators are identical. Four crosses between C tester and EAST'S material will be considered, with the families resulting therefrom.

TABLE I

EAR	CROSS	COLOR RATIO			MOTTLING RATIO		
		Predicted		Observed	Predicted		Observed
646	*PpRrCc* selfed.....	27:9:28	66:22:69	62:14:81	2:1	51:25	58:18
645	*PpRrCc* selfed.....	27:9:28	135:45:139	136:51:132	2:1	122:61	144:39
631	*PpRrCc* selfed.....	27:9:28	141:47:147	157:36:142	2:1	129:64	122:71
630	*PpRrCc* selfed.....	27:9:28	177:60:184	181:55:185	2:1	157:79	159:77
642	*PpRrcc* selfed.....	0:0:1	0:0:268	0:0:268	.....	.....	.....
643	*PpRrcc* selfed.....	0:0:1	0:0:461	0:0:461	.....	.....	.....
647	*PpRrCc*×pprrCc...	3:3:10	19:19:6	21:12:61	1:0	33:0	33:0
635	*PpRrCc*×pprrCc...	3:3:10	28:32:106	31:31:104	1:0	60:0	60:0
636	*PpRrCc*×pprrCc...	3:3:10	47:49:180	52:52:172	1:0	96:0	96:0
644	*PpRrcc*×pprrCc ...	1:1:6	8:8:49	9:9:47	1:0	18:0	18:0
652	*PpRrcc*×pprrCc ...	1:1:6	19:19:115	20:21:112	1:0	42:0	42:0
638	*PpRrCc*×PPRrCc..	9:0:7	88:0:68	74:0:72	2:1	49:25	52:22
649	PPRrCc×*PpRrCc*..	9:0:7	261:0:203	246:0:216	2:1	164:82	163:85
641	PPRrCc×*PpRrCc*..	9:0:7	159:0:123	156:0:126	2:1	104:52	106:50
640	PPRrCc×*PpRrCc*..	9:0:7	179:0:139	179:0:139	2:1	119:60	106:73
639	PPRrCc×*PpRrCc*..	9:0:7	314:0:234	313:0:235	2:1	209:104	259:54
650	PPRrCc×*PpRrCc*..	9:0:7	117:0:91	128:0:80	2:1	85:43	84:44
651	PPRrCc×*PpRrCc*..	9:0:7	224:0:174	239:0:159	2:1	159:80	161:78
648	PPRrCc×*PpRrcc*..	3:0:5	63:0:104	63:0:104	2:1	42:21	44:19

I.—pprrCc (EAST) ×PPRRcc (C tester) gave 131:0:114 with all the purple grains mottled, according to expectations. Obviously these mottled purple grains represented a PpRrCc formula, the colorless PpRrCc. The number of this ear was 315, and its further behavior is recorded in table I, in which the italicized parent represents the immediate progeny of 315. Where mottling ratios are recorded, the solid color member always precedes (2:1 means 2 solid color : 1 mottled). Table I shows that predictions on the color ratios are fulfilled in all cases, with the possible exception of ear 638; while mottling ratios are similarly according to prediction with the possible (one feels like saying probable) excep-

tion of ear 639. It is a very striking fact that where no mottling is predicted (647, 635, 636, 644, 652) absolutely none appears.

II.—PPRRcc (C tester) ×ppRrCc (EAST) gave 62:0:52 with no mottling. Half the purple grains should have had the PpRRCc formula, the other half PpRrCc; the white grains, half PpRRcc, half PpRrcc. From the latter, two ears were selfed, both giving 0:0:300.

A cross was made between an individual resulting from one of the colorless grains as female parent, and ppRrCc as male parent. Since the former could be either PpRRcc or PpRrcc, we must consider both possibilities: (1) PpRRcc×ppRrCc would give 1:1:2 and no mottling (1:0); (2) PpRrcc×ppRrCc would give 3:3:10 and a mottling ratio of 2:1. The actual ratios were 48:28:78 and 76:0, satisfying 1.

Two crosses were made between individuals resulting from two of the colorless grains as male parents, and PPRrCc as female parent. The two possibilities are: (1) PPRrCc×PpRRcc would give 1:0:1 and 1:1; (2) PPRrCc×PpRrcc would give 3:0:5 and 2:1. One of the resulting ears actually gave 115:0:134 and 78:37. The color ratio might be either 1:0:1 or 3:0:5, but the mottling ratio decides the case in favor of 1. The other ear gave 242:0:278 and 126:116. There might be a slight doubt about the color ratio, but the mottling ratio decides in favor of 2.

Two other crosses in which 2:1 mottling ratios were predicted gave 73:38 and 162:65 respectively. We may conclude that this family also fulfils the predictions fairly well. It is interesting that cases in which the color ratio may be a matter of some doubt may sometimes be decided by reference to the mottling ratio.

III.—This family resulted from a cross reciprocal to the last, or ppRrCc (EAST) ×PPRRcc (C tester). This gave an ear containing only 13 grains, so that the ratios are without significance. The same possible genotypes are confronted as under II. One of the colorless grains inbred gave, of course, 0:0:300. A single individual, produced from one of the purple grains, was used as male parent three times, once on its own silks and twice on PPRrCc. If this individual had been PpRRCc, selfing should have given 9:3:4 and no mottling, while the cross indicated should have

given 3:0:1 and 1:1. If it had been PpRrCc, selfing should have given 27:9:28 and 2:1, the cross 9:0:7 and 2:1. Actually selfing gave 207:63:90 and 270:0, clearly indicating the former. In the two cases of the cross indicated, the actual color ratios were 411:0:127 and 360:0:129. These are 3:0:1 ratios, and satisfy, as before, the formula of PpRRCc for the male parent. The mottling ratios in these cases, however, were respectively 278:133 and 235:125. Obviously, where it was felt that 1:1 mottling ratios could be predicted with some certainty, the actual ratios obtained were strikingly close to 2:1. The writer fully realizes the care which must be exercised in classifying mottled grains. These particular ears were not only shelled (as usual), but were counted twice, using the same standards as proved satisfactory elsewhere. One is forced to conclude that these additional data represent an exceptional behavior, sufficiently decisive to be of some real significance.

IV.—pprrCC (EAST) ×PPRRcc (C tester) gave unusual data. It is unnecessary to give all of them; sufficient at present are the mottling ratios obtained. Four ears resulted in which mottling was to be expected in a 2:1 ratio. The actual ratios obtained were 155:0, 30:8, 151:3, and 177:3. Obviously the usual mottling situation is absent. The question arises whether the few so-called mottled grains were truly such. It is probable that they were not, since there have been known to occur various types of anomalous grains which may readily be confused with true mottling. Had these grains occurred on ears known to contain true mottling, they would have been included in that class. I feel justified, therefore, in the tentative conclusions that (1) the P, R, and C factors of EAST and EMERSON are probably identical; (2) mottling is due to a heritable factor (or factors) which is present in EMERSON'S C tester and absent in the material of EAST, and that this factor probably behaves immediately as a dominant, no matter with which parent it enters the cross. No attempt is made at present to explain the 2:1 mottling ratios which appeared in two cases of family III instead of the expected 1:1. As for family IV, this situation may be explained by assuming that not all of the C tester material was homozygous for the presence of the mottling factor.

The R tester material was similarly crossed with EAST's material. The color ratios obtained in five small families fully satisfied the predictions. The mottling ratios obtained, however, were quite different from those before, and may be summarized as follows: (1) ten ears gave 100 per cent colorless aleurone, and, of course, no mottling; (2) there were nine ears in which the R factor, wherever present, had come in with the female parent; in these, therefore, no mottling was to be expected; these gave a total of 889 self-colored grains to 1 mottled; (3) cases in which a 2:1 mottling ratio might have been expected may be taken up separately for the different families. Family I, produced by PpRrCc (EAST) ×PPrrCC (C tester), gave three such ears, with a total of 467 self-colored: 5 mottled grains (1.06 per cent mottling; extremes 1.85 and 0.00 per cent). Family II gave four such ears with a total of 333:30 (8.26 per cent; extremes 12.12 and 5.52 per cent). Family III gave one such ear with 58:0. Family IV gave nine such ears with a total of 1840:23 (1.23 per cent; extremes 2.22 and 0.00 per cent, one case). Family V gave three such ears with 638:51, or 7.40 per cent mottling; but that is not all. One of these ears gave 263:10. The other two were identical with respect to both their parents, both growing on the same plant. One of them gave 237:41, the other 138:0.

One hesitates to draw any general conclusion from these data. Certainly R tester does not contain that essential factor for mottling which was present in C tester. In the event that EMERSON's C tester and R tester were extracted fairly recently from the same parent stock, the present situation might suggest that this unknown mottling factor was an attribute of EMERSON's R factor itself, or at least closely linked. This, however, would involve some awkward, although not impossible, assumptions to explain the behavior of mottling in those families produced by crosses of C tester with EAST's material; for, of course, the latter did not contain the mottling factor. The situation would be somewhat simplified if it were sweepingly assumed that the mottling which appeared in these R tester families (just described) was not true mottling at all, but just an imitation. True enough, mottling is at times fairly well imitated, but these particular imitations were so like the genuine

article that the writer is very reluctant to discard them. A safe tentative conclusion would be the following. The prime requisite for mottling is that the R factor enter with the male parent only; this perhaps is equivalent to saying "that the R factor be present in the endosperm in just one out of three possible doses." Under these circumstances mottling regularly occurs when there is also present that condition which is possessed and transmitted by most C tester individuals. A different condition, occurring in R tester, favors mottling in a small percentage of the possible cases, while the conditions present in EAST'S material permit of no mottling under any circumstances. The critical data should, of course, appear in the next generation.

Partial variability

The term "partial variability" has been used to indicate the variation which may occur between different parts of a single plant as regards any given character, without implying anything about the mechanism which may explain this variation. It is therefore preferable to "somatic segregation" for the present purpose. Preliminary tests of the possibility of partial variability in corn were conducted in two very simple and obvious ways. The first, so far as it went, gave such decisive and orthodox results that it may be summarized very briefly. With respect, at least, to the P, R, and C factors, pollen from suckers that had been allowed to develop was identical in crosses with that obtained from the main plant. Ears developed on such suckers were, if present, so poorly developed as to yield no adequate ratios; but ears produced on suckers that had been allowed to develop abnormally, through early removal of the main stem itself, gave the predicted ratios in all cases. These results discouraged carrying out any large scale test of this matter, at least as regards aleurone color. On the other hand, a few sporadic cases suggest that such manipulation might yield surprising results when applied to the inheritance of plant color, and particularly chlorophyll. The other method was to apply the same pollen to the silks of two of the ears on the same individual, and to compare the ratios obtained. Such attempts were frequently unsuccessful, owing to the inability of the plants

to develop two sufficiently well filled ears under the handicap of artificial pollination. Hence it was very common to get one full ear, while the other contained so few grains as to be practically worthless. This depends in part, of course, on the variety of corn used.

The bulk of the data obtained was on starchy-sweet and yellow-colorless ratios, and will be merely summarized at present: (1) the ratios were virtually identical on both ears, and (2) any marked deficiency of a given class on one ear always appeared in a strikingly

TABLE II

Ear	Count	Observed ratio	Predicted ratio
660.....	206:161	56.13:43.87	56.25:43.25
661.....	203:158	56.23:43.77	56.25:43.25
704.....	242:81	74.61:25.39	75.00:25.00
707.....	275:91	74.93:25.07	75.00:25.00
683.....	118:45	72.39:27.61	75.00:25.00
684.....	47:19	71.21:28.79	75.00:25.00
682.....	163:54	75.57:24.43	75.00:25.00
680.....	33:14	70.21:19.88	75.00:25.00
572.....	108:33	76.59:73.41	75.00:25.00
571.....	62:15	79.48:20.58	75.00:25.00
670.....	138:80	63.30:36.70	75.00:25.00
678.....	276:94	74.59:25.41	75.00:25.00
557.....	43:42	50.58:49.42	50.00:50.00
558.....	25:25	50.00:50.00	50.00:50.00

similar degree on the other ear. Relative to some of the ratios discussed earlier in this paper, representative data follow.

I. Colored-colorless ratios are markedly consistent for both ears, as may be seen from table II. The only decided inconsistency is between 670 and 678. There is little doubt that this inconsistency is real and significant, although it cannot at present be interpreted. One feels, however, like regarding this as an isolated exception.

II. Purple-red ratios are also about as consistent as could be expected (table III). Probably the only significant case is 682–680. Although the converse has been well demonstrated for other

ratios, it is altogether probable that such apparent deficiencies of red in a purple-red ratio, instead of being due merely to chance, are not only characteristic of given individuals, but heritable to some

TABLE III

Ear	Count	Observed ratio	Predicted ratio
660	155:51	75.24:26.76	75.00:25.00
661	152:51	74.39:25.61	75.00:25.00
704	182:60	75.20:24.80	75.00:25.00
707	204:68	75.00:25.00	75.00:25.00
683	89:29	75.42:24.25	75.00:25.00
684	38:8	80.85:19.15	75.00:25.00
682	132:31	80.98:19.02	75.00:25.00
680	29:4	87.87:12.13	75.00:25.00
670	101:37	73.19:26.81	75.00:25.00
678	212:64	76.81:23.19	75.00:25.00
571	52:10	80.64:19.36	75.00:25.00
572	76:32	70.37:29.63	75.00:25.00

TABLE IV

Ear	Count	Observed ratio
660	202:4	98.06:1.94
661	202:1	99.51:0.49
704	242:3	98.77:1.23
707	272:6	97.84:2.16
683	106:12	89.83:10.67
684	42:5	89.37:10.63
682	154:9	94.48:5.52
680	29:4	87.87:12.13
571	58:4	91.91:8.09
572	84:24	77.77:22.23
670	130:0	100.00:0.00
678	235:41	85.14:14.86

degree. It must be realized, however, that such deficiencies of red are probably apparent rather than real; improper classification may throw dark red grains with purple, but it may well be that the border line is thus obscured through some heritable tendency.

III. If one is to regard true mottling as limited to those cases in which the character appears in *all* the grains which receive R from the male parent only, that is, descendants of C tester, then, unfortunately, no data are at hand on comparative mottling ratios in two ears with the same parents. Such data, however, are available from descendants of R tester, where mottling (or pseudo mottling, as it may prove to be) appeared in relatively small percentages, as shown in table IV. The discrepancies apparent in table IV may be taken to indicate that the supposed mottling of the R tester line is altogether sporadic and without genetic significance. Even though that may be so, the surprising case of 670–678 is probably worthy of further investigation.

IV. Among the progeny of the faint colored grains only two poor examples of this sort are available, as may be seen in table V.

TABLE V

Ear	Count	Observed ratio
	Faint:Colorless	
562	17:46	26.98:73.02
563	26:104	20.00:80.00
557	0:42	0.00:100.00
558	9:16	36.00:64.00

It is highly probable that the occurrence of these faint grains is sufficiently limited by local conditions so that discrepancies between two such ears will prove common. This is also suggested by the results of a test which need only be briefly mentioned at present.

It is expected that the numerical value of any ratio, which is affected only by matters Mendelian, will conform with predictions based on the laws of chance. With equal certainty the laws of chance indicate that, where a 1 colored:1 colorless ratio appears, we will not find many long strings of colored grains lying together in the same row. Actually we may expect that the colored grains will be scattered within the rows of the ear in such a way that there will be, speaking relatively, n groups of 1 colored grain each, n/2 groups of 2, n/4 groups of 3, etc. These values will differ, of course, with the ratios themselves. Thus, in a 3 colored:1 colorless,

there will be n groups of 1 colorless, n/4 groups of 2, n/16 groups of 3, etc.; while, for the colored grains, there will be n groups of 1, $\frac{3n}{4}$ groups of 2, $\frac{9n}{16}$ groups of 3, etc. The exact values can easily be calculated for any ratio, although they frequently must be carried to several decimals. Such a test was applied to numerous types of ratios, and also, for purposes of control, to the tossing of coins (singly or in groups, depending on the ratio). The purpose of the test was to discover whether any of the characters under consideration were determined or limited by local conditions within the ear. Preliminary tests of this sort showed that starchy-sweet and colored-colorless ratios depended only on laws of chance. When the test was applied to the self-colored-mottled ratios of the C tester progeny, the laws of chance were fairly well satisfied, but, undoubtedly, to a less degree than in the other cases. Such slight nonconformity as occurred, however, might well have been accounted for by difficulties in classification. Tests applied to the mottling of the R tester progeny were not thought to be significant, owing to the very small percentages of the mottled grains appearing. With the particolored grains, however, very decisive results were obtained, indicating clearly that local conditions on the cob affect the appearance of this character. Thus in ears on which less than 10 per cent of the grains were particolored, the majority of the total number of such grains was made up of a few groups of 4 or 5 each. This is particularly interesting, since it has been demonstrated that this condition is heritable. The puzzle will probably be solved by finding that local conditions on the ear do not determine, but merely limit, the appearance of the particolored condition. It is expected that some, but not all, of the seemingly quite colorless grains from these ears will perpetuate the particolored tendency.

Summary

1. The use of the corn-pollinator is recommended to amateur investigators.

2. The P(Pr), R, and C factors for aleurone color, variously combined, gave predictable and readily distinguished ratios.

3. In many cases the exact genotype, with reference to the R and C factors, can be distinguished by superficial appearance.

4. The particolored grains of EAST and HAYES were identified. In these some partial substitute enables the P and R factors to express themselves, even in the absence of C. This substitute is heritable, but its effectiveness is limited by local conditions in different parts of the ear or of the plant as a whole.

5. Mottling (EMERSON), which occurs when the R factor comes in with the male parent only, is conditioned by the presence of a heritable factor or factors. This factor occurs in the C tester family, and is dominant in crosses with families which do not show mottling. The R tester family seems to contain a different factor, which produces apparent mottling only in a small percentage of the expectations.

UNIVERSITY OF CHICAGO

BULBILS OF LYCOPODIUM LUCIDULUM

R. WILSON SMITH

(WITH TWENTY-ONE FIGURES)

It is well known that certain species of *Lycopodium* belonging to that subdivision of the genus which is characterized by the non-strobilar arrangement and slight differentiation of the sporophylls produce organs of vegetative reproduction known as bulbils or gemmae. These organs are of a peculiar type, so unlike anything else in the plant kingdom that the question of their morphological nature is a very puzzling one. Various opinions have been held. They have been interpreted as equivalent to sporangia, to lateral branches in the axils of leaves, to lateral branches without supporting leaves, to reduced branches resulting from dichotomy of the stem apex and gradually displaced, and to the bulblets of certain ferns and monocotyledons.

We owe the first accurate account of the development of the bulbils to HEGELMAIER (4). He corrected the view previously held that they originate in the axils of preexisting leaves, and showed that they take the place of leaves in the phyllotactic spiral. He could find no means of distinguishing very young leaves and bulbils in longitudinal sections; and a view of the apex of the plant showed a difference only when the larger size indicated that a bulbil was beginning to develop.

STRASBURGER (10) gave a short description of the bulbils, differing from HEGELMAIER'S in some respects. In the following year, after further investigation (11), he confirmed the interpretation of HEGELMAIER in every detail but one; he thought leaves and bulbils differ somewhat in their mode of development. By special manipulation of the stem tips, he selected for study those tips on which young bulbils were present. In these young bulbils, when viewed in longitudinal section, he thought he could detect a middle apical group of two cells in the dermatogen. This account does not contradict that of HEGELMAIER, for STRASBURGER really found no difference between leaves and bulbils until the latter

were distinguishable by their greater size. My observations on this feature agree with HEGELMAIER's. I have not been able, in longitudinal sections, to distinguish a young bulbil from a young leaf until it is recognizable by the beginning of an apical meristem at its tip. STRASBURGER discussed the homology of the bulbil with considerable care, and after considering the possible explanations concluded that all the facts of development and histology are best combined in the supposition that the bulbil represents the survival of an original dichotomy ("eine einst dichotomischen Ursprung").

Much the same interpretation is given by CAMPBELL (1), who says the bulbils "are formed apparently in the axils of somewhat modified leaves. . . . . The axillary origin of the bulbils is only apparent; they are really, so far as can be determined, similar in origin to ordinary branches and formed without any relation to the leaves."

GOEBEL (3) considered the bulbils from the point of view of their adaptations rather than their homology. Although disclaiming any attempt to solve the latter, he brought forward some pertinent objections to current morphological explanations, and concluded that in their most important features the bulbils of *Lycopodium* are not unlike the bulblets of certain species of *Allium* and *Lilium*.

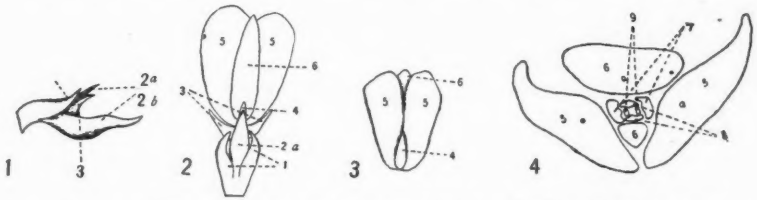
The present investigation is an attempt to help solve the problem of the bulbils by means of modern technique and serial sections which were not available to the earlier investigators. Only *L. lucidulum* has been studied, suitable material of other species not being obtainable. STRASBURGER, however, found that there is a great similarity in the bulbils of the six species which he compared, and it is probable therefore that the following account with only minor changes will hold good for all.

Description of bulbils

Two parts must be distinguished in the bulbil: the base which remains attached to the stem of the plant for many years and does not store up nutriment; and the distal part, or bulbil proper, which is heavily laden with starch grains, and which, when mature,

separates from the base and readily gives rise to a new plant. Between the two parts is a narrow neck which breaks easily when the bulbil is ripe. The young bulbil has a small apical meristem at its tip, and as it grows produces decussate pairs of protuberances, which in their relation to the bulbil axis resemble foliar organs, but in maturity differ more or less from typical leaves. The base has three pairs of these and the bulbil proper about six.

From the bulbil primordium there arise, as described by HEGELMAIER from external appearances, first a pair of small leaves, laterally situated, but soon displaced toward the stem apex; then from the growing point between these a median pair, and soon after them another lateral pair, not displaced. The median pair, especially its abaxial member, is much the largest. This larger



FIGS. 1–4.—Fig. 1, side view of bulbil base; ×3; fig. 2, bulbil and base from upper side; ×3; fig. 3, bulbil proper from lower side; ×2.5; leaves numbered in order of appearance; *2b*, "supporting" leaf; fig. 4, cross-section of tip of bulbil; leaves numbered in order of appearance; ×10.

outer leaf becomes the so-called "supporting" or "cover" leaf of the bulbil (figs. 1, 2). HEGELMAIER was unable to decide whether the further axis of the bulbil is the direct continuation of the primordium, and the supporting leaf therefore truly lateral, or whether the supporting leaf is the direct continuation of the primordium, and the bulbil proper therefore an outgrowth and truly lateral.

The first leaves of the bulbil proper are dorsal and ventral; the second pair, which are lateral in origin, gradually turn their upper edges outward and assume a dorsiventral relation; the third pair are median, long, and narrow (figs. 2, 3). These three pairs of leaves are fleshy, and the leaves of the second pair are also much modified in form. The remaining leaves of the bulbil

are small and closely arranged about the growing point (fig. 4). The axis of the bulbil proper develops endogenously two small rootlets, which remain imbedded in the fleshy leaves until the germination of the bulbil, when they push out into the soil.

Anatomy of stem apex and bulbils

L. lucidulum has only one mode of branching, namely, by dichotomy of the apex. The growing point of the stem tip is broad and flat, or slightly raised in the center, and is surmounted and protected by the more rapidly lengthening leaves. In *Lycopodium* there seems to be a relation between the form of the growing point and the rate of growth. Slow growers, such as *L. lucidulum* and *L. Selago*, have the apex as described (fig. 6); while rapid

FIGS. 5–8.—Fig. 5, tangential section of bulbil: r_1 and r_2, roots; 5, fleshy leaves; ×5; fig. 6, apex of stem: *sp*, young sporangium; ×38; fig. 7, beginning of dichotomy of stem in longitudinal section; ×38; fig. 8, more advanced stage of same; ×23.

growers, such as *L. clavatum*, *L. annotinum*, and *L. alopecuroides*, have the apex conoid in form and considerably in advance of the youngest leaves. Before the apex branches it becomes wider (there is considerable variation in the width of the growing point without any apparent relation to branching). The initial cells of the middle region now cease to grow and multiply, while those on either side continue their activity (fig. 7). Soon the two growing points, separated by a cleft, begin putting forth leaves on all sides (fig. 8). In longitudinal section it can be seen that the central cylinder has divided into equal strands, and the two apices are similar in all respects.

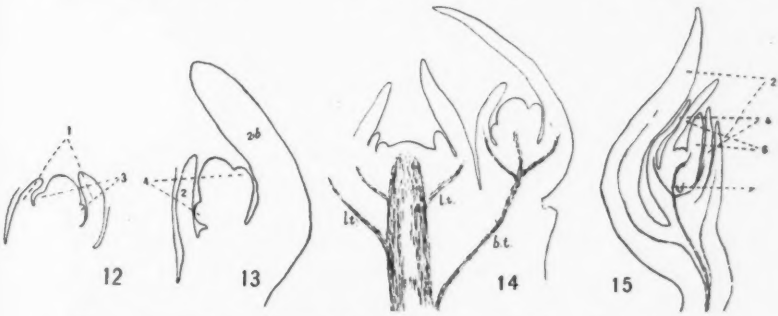
In cross-sections the equality of the two branches is just as apparent. Fig. 9 shows a section of the central cylinder below a dichotomy at a distance of about half a year's growth from the two tips. The central part of the cylinder is filled with immature tissue, which can be distinguished approximately into xylem and phloem areas. The shaded areas represent fully differentiated xylem made up on the outer side of protoxylem tracheids, and on the inner side of larger metaxylem elements. As differentiation proceeds in this species, the metaxylem portions meet in the middle of the cylinder and become more or less continuous, and the phloem occupies the indentations or bays between the xylem strands. Surrounding the cylinder there is a clearly marked endodermal sheath in the form of an irregular layer of cells, only the inner contiguous walls of which are thickened at this stage of

FIGS. 9–11.—Cross-sections of central cylinder of forking stem, xylem areas shaded; small cross-hatched areas indicate leaf traces; ×52.

development. In fig. 11 the whole sheath is shown, but in figs. 9 and 10 only the thickened cutinized walls are to be seen. As the dichotomy proceeds the xylem strands change position but little, the sheath from opposite sides pushing inward until the division into two similar cylinders is complete. In this mode of branching no branch gaps of any kind are formed in the sheath or xylem or phloem. The length of stem between figs. 9 and 10 was 0.65 mm.; and between figs. 10 and 11 it was 0.5 mm. It will be noted that there are eight xylem strands in fig. 9, and that in each of the two branches there are five. The new strands are not formed by a division of old ones, but arise *de novo* out of meristematic tissue. The beginnings of these strands may be seen in fig. 10.

As shown by JONES (**5**), the protoxylem strands in *Lycopodium* are constant neither in number, shape, nor position. New strands

may arise either by branching of preexisting strands, or from the meristem. I have also found that a strand when traced upward may gradually diminish in size and ultimately disappear. In the stem of which figs. 9, 10, and 11 are sections, the leaves were 9-ranked, and this ranking continues in both the branches, notwithstanding the reduction of protoxylem strands from nine to five. As shown many years ago by CRAMER (2) and HEGELMAIER (4), there is no relation between the number of orthostichies and the number of xylem strands. The leaf traces of *Lycopodium*, so far as they have been investigated, are mesarch in structure (7, 8). They are so in *L. lucidulum*. The trace separates very gradually



FIGS. 12–15.—Fig. 12, tangential section of young bulbil: *1*, first pair, *3*, third pair of lateral leaves; fig. 13, radial section of bulbil rather older than fig. 12; *2*, first pair of median leaves; *4*, first leaves of bulbil proper; ×38; fig. 14, longitudinal section of stem tip and young bulbil: *2b*, "supporting" leaf; *lt*, leaf trace; *bt*, bulbil trace; ×23; fig. 15, longitudinal section of older bulbil, leaves numbered in order of appearance; *r*, root tip; ×10.

from the protoxylem of the central cylinder, traverses the pericycle for a short distance, and then pierces the endodermis, after first pushing it out into the form of a little pocket (figs. 10, 11). The separation of the leaf trace causes no gap or disturbance in the central cylinder. Immediately above and below the point of exit the sheath closes. The leaf trace at first consists only of spiral tracheids, but later is surrounded by deeply staining cells, presumably phloem.

The vascular strand of the bulbil does not at all resemble that of a branch. It is a single strand, similar in every way to a leaf

In cross-sections the equality of the two branches is just as apparent. Fig. 9 shows a section of the central cylinder below a dichotomy at a distance of about half a year's growth from the two tips. The central part of the cylinder is filled with immature tissue, which can be distinguished approximately into xylem and phloem areas. The shaded areas represent fully differentiated xylem made up on the outer side of protoxylem tracheids, and on the inner side of larger metaxylem elements. As differentiation proceeds in this species, the metaxylem portions meet in the middle of the cylinder and become more or less continuous, and the phloem occupies the indentations or bays between the xylem strands. Surrounding the cylinder there is a clearly marked endodermal sheath in the form of an irregular layer of cells, only the inner contiguous walls of which are thickened at this stage of

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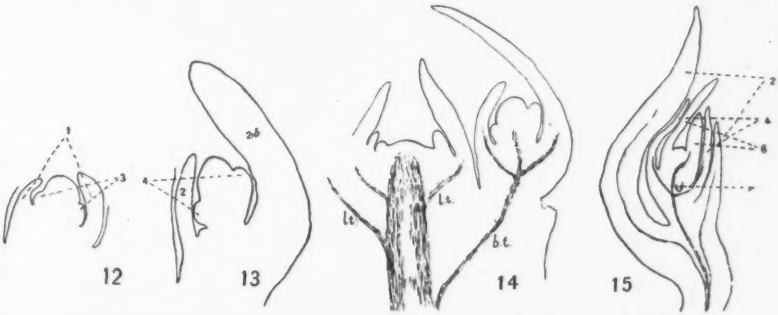

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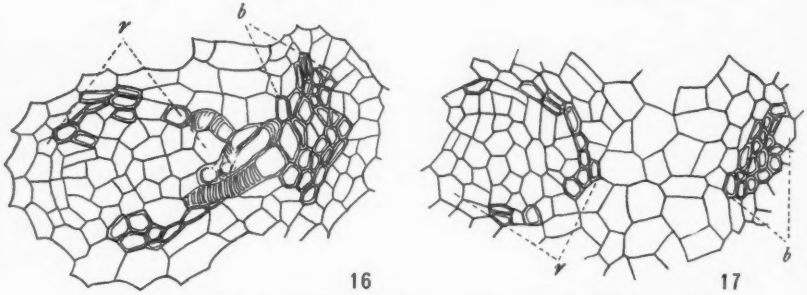
The vascular strand of the bulbil does not at all resemble that of a branch. It is a single strand, similar in every way to a leaf

trace in its relation to the central cylinder and its passage through the cortex (fig 14). Not until it reaches the outer part of the cortex or the decurrent base of the bulbil does it exhibit any essential deviation from a leaf trace. Here it widens into a narrow tangential band of cells, and presently gives off laterally two small traces to the first leaves of the bulbil (fig. 12). The middle part continues and presently widens into a radial band whose outer portions become the traces of the second pair of leaves (figs. 13, 15), and so on until four pairs of traces have separated from it. These facts make it clear that the "supporting" leaf is undoubtedly a lateral organ. In the bulbil proper in connection with the appearance of

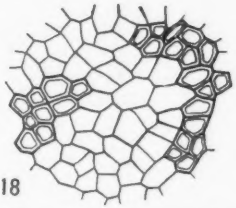


FIGS. 16, 17.—Fig. 16, cross-section of vascular bundle of bulbil where first root is given off; ×320; fig. 17, cross-section of bundles of bulbil and root below origin of root: *b*, bulbil bundle; *r*, root bundle; ×320.

the first root a much greater change occurs. In a young bulbil, even before the vascular tissues are differentiated, the tip of this root is outlined as a mass of deeply staining meristematic cells. A second and smaller root develops nearer the tip of the bulbil (fig. 5). Both of these roots connect with the vascular strand of the bulbil on its adaxial side and, turning downward and laterally, remain imbedded in the parenchyma and separated from it by slime and crowded tissue.

Fig. 16 shows the junction of the root cylinder and the axis of the bulbil, and fig. 17 is a section below this. In both of these it can be seen that the bulbil axis is still essentially a leaf trace, but above the junction of root and axis all resemblance to a leaf trace is lost. The arrangement of the tracheids is somewhat like

that of a root, but much more irregular. Sometimes it is distinctly diarch (fig. 18), more commonly it is horseshoe-shaped, and sometimes almost a complete ring, often with a few tracheids in the center (fig. 19). Surrounding the whole xylem area there are one or two irregular layers of cells, probably a pericycle, and outside these an indistinct sheath (this feature is shown only in fig. 16). This irregular arrangement continues until the fifth and sixth pairs of leaf traces are given off and also the second root. Above that the tissues are still meristematic in the ripe bulbil. The bulbil, like the leaves, is well supplied with stomata, and photosynthesis proceeds actively. The cause of the accumulation of starch in the bulbil proper and not in the base seems to lie in the absence of phloem in the neck of the bulbil. Here the cells are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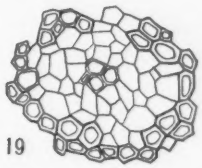
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FIGS. 18, 19.—Cross-sections of bundle above origin of first root; ×320

entirely wanting which elsewhere in the bulbil surround the xylem strand, and which I have regarded as phloem, although the sieve plates have not been identified. The detachment of the bulbil proper is brought about by a disorganization, apparently a gelatinization, of the walls of the xylem cells in the neck.

When a ripe bulbil is kept on damp soil it soon germinates. Both roots penetrate the soil and branch repeatedly, and from the tip of the bulbil a slender stem is put forth. On this stem the new leaves, although scattered, are from the first arranged spirally. JONES (5) traced the development of the vascular cylinder in the young plants growing from bulbils of *L. Selago* and *L. serratum*, and concluded that the original simple bundle becomes successively diarch, triarch, etc., by division of the xylem. My observations on *L. lucidulum* do not agree with this conclusion. I find, in agreement with JONES, that the young stem at its attachment with

the bulbil is diarch, having two masses of xylem with one phloem mass between, but followed up for nearly an inch, it never becomes triarch. The xylem becomes horseshoe- or ring-shaped, much as in figs. 17 and 19, changing constantly, and there is no hint as to how the multiprotoxylic condition of the adult stem arises. The irregularity and continual change in the xylem of these young stems are comparable to the conditions described by Miss WIGGLESWORTH (12) in young *Lycopodium* sporophytes growing from gametophytes.

HEGELMAIER'S statement that the bulbils replace leaves in the phyllotaxy is confirmed by an examination of the relation of bulbil and leaf traces. On following these back in cross-sections to their junctions with the xylem strands of the central cylinder, the bulbil traces are found in close succession. In many cases they represent successive leaves; in other cases a leaf trace stands between two bulbil traces; but in every case examined the bulbil traces all fell within a single leaf spiral.

Conclusions

1. The bulbil is not the homologue of a branch, since it has a simple vascular strand with mesarch concentric arrangement; whereas branches have a vascular system with complex exarch radial arrangement. Furthermore, it is not a reduced dichotomy or the equivalent of the bulblets of *Lilium* or *Allium*.

2. It is not the homologue of a sporangium, for the reason, among others, that it receives a prominent vascular strand, a feature which is lacking in the sporangia of all Lycopodiales.

3. It is a transformed leaf, retaining the position, dorsiventrality, and in great measure the vascular strand of a leaf. It may perhaps be homologized with the bulblet of a fern produced so early in the history of the leaf bearing it that the latter exhibits the leaf character only while inside the cortex of the stem.

Further observations on the bulbils and habits of L. lucidulum

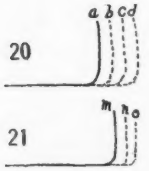
In the literature of the subject, I do not find any recognition of the periodicity of the bulbils. In *L. lucidulum* they are quite as responsive to season as the sporangia. The latter begin to form

in autumn in preparation for the next year, and continue to form when growth is renewed in the spring. Then, beginning some time in June, for more than two months the apex develops a succession of sterile leaves, in the midst of which two to four bulbils may make their appearance, always near each other and on one side of the stem, on that side of a branch which is farthest from the other branch. The primordia of the bulbils increase rapidly in size, pointing vertically upward at first like the young leaves, and then gradually becoming horizontal. They reach maturity in September. Since the bulbils are formed but once a year and their bases are persistent, it follows that they furnish a means of measuring the annual increment of growth in length. There are other but less accurate means of estimating a year's growth, by the old sporangia whose walls do not completely disappear for several years, and also by a difference in the length of sporophylls and sterile leaves. The annual growth in plants bearing bulbils can be determined quite easily for the last ten or twelve years, and in some cases even for twenty years. It is surprisingly small, averaging about one inch.

The possibility of determining the age of any given part of the stem leads to some interesting observations. For instance, it can be shown that the metaxylem matures very slowly, not being fully differentiated until well into the second year. The cortical zones, characteristic of most *Lycopodium* stems, are not differentiated until the third year. It is also possible to calculate the frequency of dichotomy of the stems. The commonest interval between successive dichotomies is four years, but intervals of two, three, five, and six years also occur frequently. I have never found a stem branching in two consecutive years.

Like several other species, *L. lucidulum* has the old stem horizontal and rooted, and the young and greener stem upright. By means of the bulbil bases it is clearly shown that the upright part is six or seven years old. Observations from year to year show that the plants, although adding annually one inch to their length, maintain the same average height. Each year a part of the erect stem, equaling a year's growth, becomes curved and finally horizontal. Fig. 20 represents the situation in four

successive years. Decapitated plants are not killed, but, having no means of renewing the apical meristem, they cease to grow or divide. Fig. 21 represents such a decapitated stem in three successive years, the upright portion shortened each year by the equivalent of a year's growth. Whether such a stem will finally become altogether horizontal, I do not yet know, nor have I yet been able to discover the cause of the regular change in direction from upright to horizontal. Observations in the field seem to show that root contraction is not the determining cause (stem tips decapitated in 1915 were found to be dead in the summer of 1919).



FIGS. 20, 21.—Fig. 20, diagram representing position of plant four successive years; fig. 21, diagram representing position of decapitated plant three successive years.

Some interesting data can also be gathered in regard to the behavior of the roots. These, as in many other species of *Lycopodium* whose tips are erect or sloping (**6, 7, 9**), do not pass straight out through the cortex, but turn downward. In *L. Selago* these roots "arising at the apex pass obliquely, then directly down through the middle cortex and only appear at the outside beneath the soil" (**6**). The same description is true of *L. lucidulum*, except that the roots do not originate at the apex, but begin at some distance behind the apex; how far behind is not clear. They rarely form within the first year's growth. Apparently they increase in number in the older parts of the erect stem; but as small roots might easily be overlooked in freehand sections, I am not quite certain that new roots may form in parts of the stem as old as five or six years. These roots, in the upright part of the stem, remain small, usually less than 6 mm. in length. As they do not emerge to the outside until in a part of the stem at least six or seven years old, it is evident that they must be in a dormant or slowly growing condition within the cortex for as many as two to five years. The downward growth in the cortex is not very great, the distance between the junction with the central cylinder and the point of emergence to the outside varying from 6 to 15 mm. Reaching the soil, they grow rapidly, quickly reaching a length of several inches.

Summary

1. The origin and vascular bundles of branches, leaves, and bulbils are described, and the conclusion is reached that the bulbil is comparable to a leaf rather than to a branch.

2. The accumulation of starch in the bulbil proper is ascribed to the absence of phloem in the narrow neck joining it to the base, and the detachment of the ripe bulbil to the disorganization of the xylem walls in this region.

3. The rate of growth is estimated from the persistent bases of the bulbils, and observations are made on the habits of the plant.

McMaster University
Toronto, Canada

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TENDRILS OF SMILAX[1]

AGNES ARBER

(WITH PLATE XXII)

The nature of the tendrils of *Smilax* has excited perhaps more controversy than almost any other problem arising out of the normal vegetative morphology of flowering plants. It is unnecessary to deal here in detail with the voluminous literature which has grown up about the subject, since this task has been excellently performed by DOMIN (4), who himself holds the opinion that the tendrils are trichome structures, an opinion which does not seem to the writer to be well founded. It will suffice to group together the various alternative views which he has enumerated, and to attempt to test them, from the standpoint of the phyllode theory (1), by a study of a typical species, *Smilax herbacea* L. (fig. 1). The views which different authors have promulgated may be considered as follows, under five heads:

1. That the *Smilax* tendrils are metamorphosed stipules, or outgrowths of the apical region of the leaf-sheath.

Both these possibilities seem to be excluded by the fact that the tendrils arise from the petiole, immediately above the sheath, it is true, but entirely disconnected from it both externally and as regards their vascular system.

2. That the *Smilax* tendrils represent a bipartite ligule, each tendril being a demi-ligule.

This alternative is ruled out because, as GLÜCK (5) and DOMIN (4) have shown, there is occasionally a definite ligule in addition to the tendrils. It is also discounted for the same reasons that make the first view untenable.

3. That the *Smilax* tendrils are either metamorphosed leaflets, segments, or lobes of a compound leaf, or lateral free nerves which become detached before the others.

[1] This paper represents part of the work carried out during the tenure of a Keddey Fletcher-Warr Studentship of the University of London, and with the aid of a grant from the Dixon Fund of the University of London. The writer wishes to acknowledge her indebtedness for material to Miss G. Lister, Professor Seward, and the Curator of the Cambridge Botanic Garden.

If any of these related alternatives held good, we should expect to find the vascular structure of the tendril showing some affinity with the vascular structure of the midrib or lateral veins of the "lamina" of the *Smilax* leaf. The midrib and lateral veins of the blade, however, are each characterized by an arc of bundles (fig. 4), while the tendrils have an irregular closed ring (fig. 3 *B*).

4. That the *Smilax* tendrils are metamorphosed trichomes or emergences.

The high development of the vascular system of the tendrils seems to make it impossible to accept this theory. The emergences on the stem of *Smilax* itself, which on this view must be homologous with the tendrils, are non-vascular, as are the paired glands at the base of the leaf of *Tamus communis* L., whose position at first glance suggests a comparison with the tendrils of *Smilax*.

5. That the tendrils of *Smilax* represent "un double prolongement latéral des éléments cellulo-vasculaires du pétiole."

This view, which was suggested by CLOS (**2**) more than half a century ago, and has been more recently supported by GLÜCK (**5**), seems to contain the germ of the true explanation, although, in the form in which CLOS enunciates it, it is essentially descriptive rather than morphological. The writer wishes to propose a related but more comprehensive view, which interprets each of the tendrils of *Smilax* as equivalent in morphological value to the petiole, and as having originated through a dédoublement or chorisis of that organ.

An analogy may perhaps be suggested with the stamen phalanges of *Hypericum Elodes* Huds., which sometimes consist of three members, and which very probably have arisen by secondary chorisis of an ancestral single stamen. A closer analogy is indicated by QUEVA'S (**7**) comparison between the anatomy and insertion of the tendrils of *Smilax* and the stalks of the leaflets of certain Dioscoreaceae with compound leaves. It seems by no means impossible that, in this family, the compound character of the leaf may also be due to chorisis of the petiole giving rise to three equivalent organs.[1]

[1] The writer hopes to deal in a later paper with the general subject of "compound" leaves among monocotyledons, and to discuss the part which chorisis may have played in their origin.

It is unnecessary to follow the relations of the vascular system of the petiole and tendril of *Smilax* in detail, since this has already been done by QUEVA. The general equivalence of the vascular structure in these organs is shown in fig. 3 *B*. It may perhaps be objected that the occurrence of a ring of bundles in the *Smilax* tendril, instead of being an indication of homology with the petiole, may merely represent that skeletal arrangement which best enables the tendril to perform its special function. The weight of this criticism, however, is lessened when we realize that in the leaf tendrils of another member of the Liliaceae (*Gloriosa superba* L., fig. 6), which approach radial symmetry in their external form quite as closely as do the tendrils of *Smilax*, the plan of the vascular system remains purely dorsiventral, although the amount of xylem increases considerably in passing from the lamina to the tendril (figs. 7, 8). The leaf tendrils of *Fritillaria verticillata* Ledebour, and of *Polygonatum cirrhifolium* Royle, resemble that of *Gloriosa* in structure.

According to the phyllode theory advocated by the writer (1), the blade of *Smilax* is not equivalent to the lamina of a dicotyledon, but is merely a "pseudo-lamina" representing an expansion of the upper region of the petiole. The thickened tip (fig. 5 *ap*) which characterizes the blade of some members of the genus, for example *S. mauritanica* Poir., is possibly the last relic of the unexpanded petiolar apex. Each tendril on this interpretation is equivalent to the *petiole+pseudo-lamina*. On the other hand, in *Gloriosa* the leaf seems to be reduced to the sheath or leaf-base alone, the tendril representing the specialized tip of this leaf-base.

Petiolar tendrils, with the blade entirely, or almost entirely, aborted, are not unknown among dicotyledons, as, for example, the first leaves of a species of *Tropaeolum* described by DARWIN (3). In connection with *Smilax*, it is perhaps significant that a tendency to torsion of the petiole or leaf-base is by no means rare among monocotyledons. Cases are known, for instance, in the Commelinaceae, Amaryllidaceae, Zingiberaceae, and Gramineae, as well as in the Liliaceae, to which *Smilax* belongs (6). In most of these instances the torsion, even in the extremest examples, merely leads to resupination of the leaf; but in *Gloriosa* this power

of twisting of a region which, although now apical, seems in reality to be part of the leaf-base, has been utilized in tendril formation. It is interesting that *Polygonatum* includes both species with twisted leaves and also species whose leaves have tendril apices resembling those of *Gloriosa*. Similarly in *Smilax* the torsion capacity of the petiole seems to have fulfilled itself on specialized lines in the production of a climbing organ.

It may be noted in passing that the blade of *Smilax* often conforms to a shape which is one of the most characteristic among those adopted by the pseudo-lamina of monocotyledons, its outline being entire and more or less ovate, with a base which is cordate or somewhat sagittate (fig. 1). Forms of this type, as has been pointed out in a previous paper (1), are not only known in the Liliaceae, but recur in the Alismaceae, Pontederiaceae, Dioscoreaceae, Araceae, and Orchidaceae. This list may now be increased by the addition of *Cyanastrum cordifolium* Oliver, of the Haemodoraceae, and certain species of *Commelina* among the Commelinaceae.

To the writer, the whole organization of the leaf of *Smilax* is best explained according to the phyllode theory, and the interpretation suggested has been reached from this standpoint. At the same time, however, the view here propounded, of the origin of the tendrils of this genus through chorisis of the petiole, in no way depends upon this general theory. There is nothing to prevent its independent acceptance by those who do not share the conviction that the leaves of monocotyledons are invariably of the nature of petiolar or leaf-base phyllodes.

Summary

In this paper the conflicting views hitherto held regarding the nature of the tendrils of *Smilax* are briefly considered, and it is concluded, on grounds of anatomy and external morphology, that these tendrils are equivalent to the petiole in morphological value, and have arisen through chorisis or dédoublement of that organ.

Balfour Laboratory
Cambridge, England

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EXPLANATION OF PLATE XXII

In all sections xylem is indicated in black, and phloem and undifferentiated bundles in white.

FIG. 1.—*Smilax herbacea* L.: single leaf showing sheath (*s*), tendrils (*t*), and petiole (*p*); ×⅔.

FIG. 2.—*Smilax herbacea* L.: *A*, transverse section of very young lamina and accompanying tendrils; vascular tissue too young to be well differentiated; petiole as yet undeveloped; *B*, actual attachment of tendrils; these sections illustrate large size of tendrils relative to lamina in embryonic stage; ×31 circa.

FIG. 3.—*Smilax herbacea* L.: transverse sections of mature leaf; *A*, through leaf sheath; *B*, through petiole and tendrils, showing relative orientation of organs; ×19 circa.

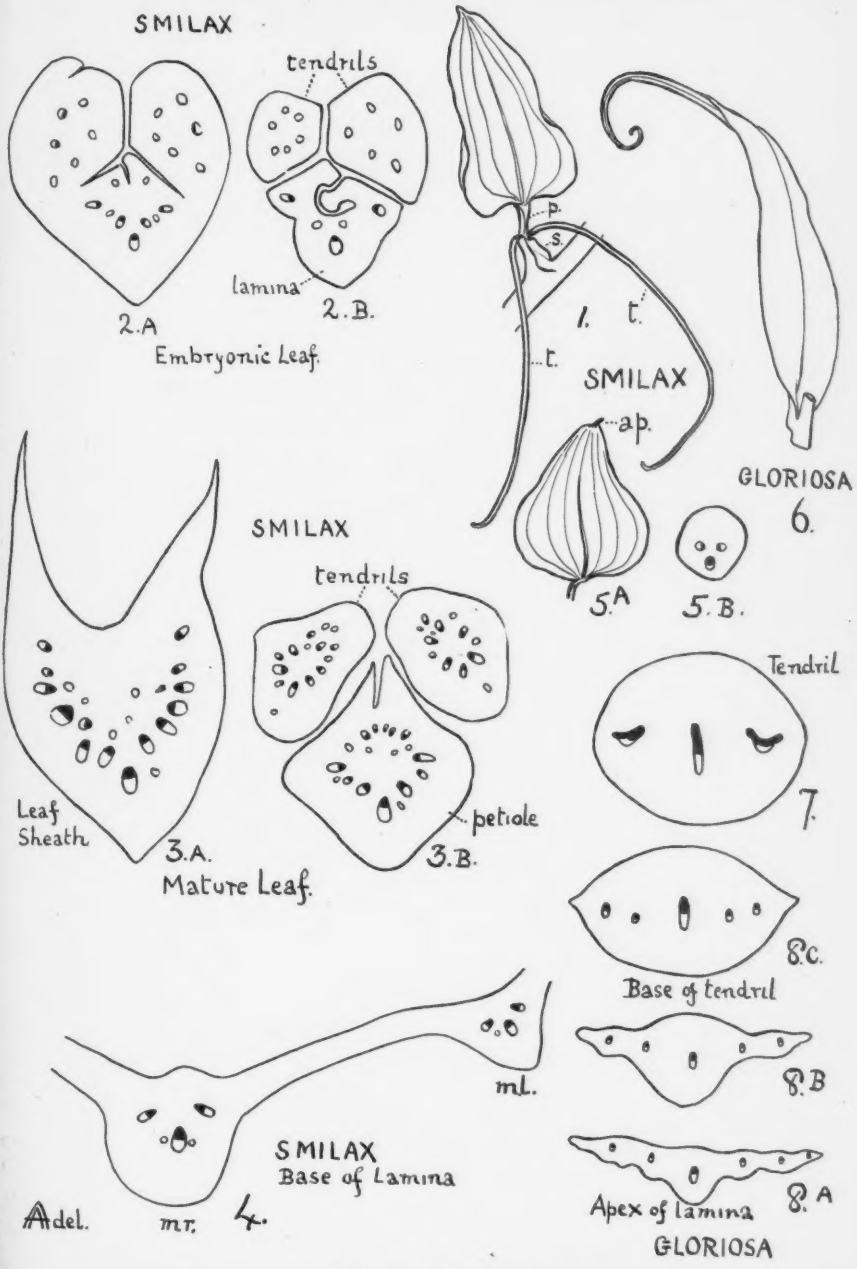
FIG. 4.—*Smilax herbacea* L.: transverse section close to base of lamina passing through midrib (*mr*) and main lateral (*ml*); ×19 circa.

FIG. 5.—*Smilax mauritanica* Poir.: *A*, pseudo-lamina with thickened apex (*ap*); ×⅔; *B*, transverse section through apex; ×19 circa.

FIG. 6.—*Gloriosa superba* L.: leaf with apical tendril; ×⅔.

FIG. 7.—*Gloriosa superba* L.: transverse section through tendril; lateral veins fused so that only midrib and 2 laterals show; ×31 circa.

FIG. 8.—*Gloriosa superba* L.: transverse sections of another leaf showing transition from apex of limb (*A*) to base of tendril (*C*); ×31 circa.



ARBER on SMILAX

CURRENT LITERATURE

MINOR NOTICES

Engler's Syllabus.—The seventh edition of Engler's *Syllabus*[1] had marked a great progress beyond the sixth; 135 pages of text had been added and the usefulness of the book was greatly increased by the introduction of illustrations. No such radical changes were made in favor of the eighth edition, which appeared in the summer of 1919. The number of illustrations remained the same, although some were replaced by new ones, and the text was only increased by 11 pages. A few groups, for instance the gymnosperms, show considerable changes. Here the fossil families have received more attention. The Cycadofilicales, which were not mentioned in the seventh edition, are now discussed. Also the Filicales are rearranged and are now headed by the Marattiales. Comparatively few changes are made in the angiosperms. The chapters on plant classification and the outline of floral regions are rewritten by ENGLER himself, and the new literature finds consideration throughout the book. Probably ENGLER and GILG did the best they could while handicapped by lack of literature from English speaking countries.

The rapid growth of the *Syllabus* from edition to edition has undoubtedly suffered a setback through the war. Nevertheless, the book is still the most convenient outline of the generally accepted system which bears ENGLER'S name, and as a very handy index to his *Natürliche Pflanzenfamilien* it remains indispensable to the student of botany. It might be added that its price for American purchasers is about 150 marks.—A. C. NOÉ.

A dictionary of botany.—SCHNEIDER and LINSBAUER'S[2] dictionary of botany lists about 7000 technical terms which are accompanied by short definitions and cross-references, or by articles of sometimes considerable length. SCHNEIDER had published the first edition with the help of a large staff of collaborators, and the second edition was left to the care of LINSBAUER, who is HABERLANDT'S successor in Graz (Austria). The text is preceded by a short bibliography of botanical treatises and periodicals. Only German books are listed, and the *Annals of Botany* and the BOTANICAL GAZETTE are the only English and American periodicals which are mentioned. Most illustrations are rather old and well known to all students of botany. Modern plant morphology is largely neglected, except that the embryology

[1] ENGLER, ADOLF, and GILG, ERNST, Syllabus der Pflanzenfamilien. 8. Auflage. 8vo. pp. xxxv+395. *figs.* 457. Berlin. 1919.

[2] SCHNEIDER, C. K., and LINSBAUER, KARL, Handwörterbuch der Botanik. 2. Auflage. 8vo. pp. xxi+824. *figs.* 396. Leipzig. 1917.

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of the gymnosperms and angiosperms contains a few illustrations from articles by CHAMBERLAIN and Miss PACE which had been published in the BOTANICAL GAZETTE. The articles on paleobotany were first written by POTONIÉ, after whose death they were revised by KUBART in Graz. In these articles the work of SEWARD is never mentioned, and SCOTT is hardly considered. The articles on plant genetics are more up-to-date, and best of all are those on physiology and anatomy.

The lack of knowledge with regard to American and English botanical literature is very pronounced in many German publications. The geologists in Germany know more English because they have to read the publications of the U.S. Geological Survey.—A. C. NOÉ.

Origin and development of Compositae.—SMALL[3] has assembled in book form his papers on the origin and development of the Compositae, which appeared in the *New Phytologist* during 1917-1919. It is an application of our knowledge of evolution, heredity, and geographical distribution to the immense amount of material presented by this great family. This study has been carried on for ten years, and "in so far as success has been achieved in the unravelling of the tangled skein of descent of this particularly large group of angiosperms, it is due to the recognition of new criteria and the critical revision of the old criteria."—J. M. C.

Joseph Dalton Hooker.—BOWER[4] has written a most interesting account of Sir JOSEPH DALTON HOOKER for the series of booklets issued by the "Society for Promoting Christian Knowledge," under the general title "Pioneers of Progress," and the subtitle "Men of Science." The titles of the brief chapters suggest the contents: Birth and education; Foreign travel; Kew; Authorship; The species question; Personal characteristics; Hooker's position as a man of science. The author and his style form a combination that insures authoritative statements and interesting presentation.—J. M. C.

Flowering plants and ferns.—Under this title WILLIS published the first edition of his manual and dictionary in 1897. A second edition appeared in 1904, a third in 1908, and now a fourth edition has been published.[5] The purpose is to supply a convenient summary of information about plants, and the result is a very convenient book of reference. The most noteworthy feature of the present edition is the incorporation of all the parts of the earlier editions

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[3] SMALL, JAMES, The origin and development of the Compositae. pp. xi+334. *pls. 6*. London: William Wesley & Son. 1919.

[4] BOWER, F. O., Joseph Dalton Hooker. pp. 57. New York: Macmillan Co. 1919.

[5] WILLIS, J. C., A dictionary of the flowering plants and ferns. Fourth edition. pp. xii+712+liv. Cambridge: The University Press. 1919. New York: G. P. Putnam's Sons.

into one general dictionary, and the omission of the former part dealing with morphology, classification, geographical distribution, economic uses, etc. There are approximately 20,000 entries, so that a wealth of information is available at a minimum of trouble.—J. M. C.

NOTES FOR STUDENTS

Tropical rain forests.—Two recent contributions have added considerably to our knowledge of the ecology of tropical rain forests, especially as both present quantitative data concerning habitat and also the vegetation. The first by BROWN[6] deals with the vegetation of a portion of the Philippine Islands, and the second by MCLEAN[7] with some of the rain forest near Rio de Janeiro, Brazil, and is the continuation of a report already noticed.[8] This rain forest of Brazil is regarded as the climax type for a large portion of the country. A biological spectrum of the Raunkiaer type would show an enormous preponderance of woody plants arranged in three distinct strata, the ground flora being comparatively open. There is a great diversity of species, with the Leguminosae as the most prominent family, and the Rubiaceae and Piperaceae important among the undershrubs. Ferns and lycopods are largely limited to rocky spots. Conspicuous flowers are abundant in the upper canopy and notably lacking below. Buttressed tree trunks are rare, in spite of the frequency of violent winds, but thorny stems are frequent even in large trees. The floristic diversity and the contrasting uniformity of appearance, especially in leaf form, are ascribed to (1) the antiquity of prevailing conditions, and (2) the peculiarity of the environment. The soil is shallow and pervious, with a water-holding capacity of about 40 per cent, and an average water content of 10 per cent. It is deficient in mineral nutrient material and particularly in calcium carbonate. The humus content is about 3 per cent. *Mycorhiza* are very abundant. A very considerable amount of rain is intercepted by foliage and evaporated into the air, thus reducing the rainfall efficiency. Light measurements made with photographic exposure meters show the average ratio of the light outside and that within the deep forest to be 1:0.06; some spectroscopic measurements, however, tend to show that the photosynthetic efficiency of the shade illumination is relatively greater than the actinic.

The leaves of the forest are in general characterized by their larger size, the small number per plant, and the frequency of nyctitropic movements and of the vertical position. The shade leaves show conspicuous water-storing epidermis, reduced and undifferentiated mesophyll, and occasional epidermal

[6] BROWN, W. H., Vegetation of the Philippine Mountains. Dept. Agric. and Nat. Resources, Bur. Sci. Pub. **13**:434. *pls. 41. figs. 30.* Manila. 1919.

[7] MCLEAN, R. C., Studies in the ecology of tropical rain forest; with special reference to the forests of South Brazil. Jour. Ecol. **7**:121–172. *figs. 10.* 1919.

[8] BOT. GAZ. **69**:92–94. 1920.

papillae. The leaf area of the sun foliage is approximately the same as that of the shade leaves, but the latter are decidedly larger and narrower. Red coloration is common in the young shade leaves, and such leaves are shown to have a higher rate of respiration. The percentage of carbon dioxide within the forest is shown to be high, and here light is doubtless the limiting factor of photosynthesis.

BROWN agrees with MCLEAN in recognizing valley and mountain forest types, and in addition describes a distinct transition form. The lowland type of the part of the Philippines under consideration is the Dipterocarp forest and extends to an altitude of 600 m. It exhibits distinct strata or stories composed of vegetation 40, 20, and 10 m. high respectively. Epiphytes are largely phanerogams, and are confined chiefly to the largest branches of the tallest trees. Buttressed trees and cauliflora are developed by many species, while the ground covering is characterized by rattans in the rosette stage. On a typical plot there were 22 first story species, 43 second story species, and 23 lower story species.

The midmountain forest extends from 600 m. to an elevation of about 900 m. and shows two stories of about 18 and 8 m. in height. One typical association is termed the *Quercus-Niolitsea* forest from the most abundant genera. The undergrowth is less dense, but the ground cover of ferns and herbaceous plants is better developed than in the Dipterocarp forest. Epiphytes are also more abundant, and include more cryptogams. Above 900 m. a montane forest is developed, exhibiting a single stratum of vegetation some 10 m. high, and known as the "mossy forest" from the great abundance of mosslike plants.

As developed on Mt. Maquiling this last may be termed a *Cyathea-Astronia* association from the two most prominent genera. The herbaceous ground cover is dense; mosses, filmy and other ferns, *Selaginella*, orchids, and lianas are abundant, many growing as epiphytes. Trees are low and contorted in habit. Statistical analyses are made of all types of forest, the size of the trees as well as their floristic relationship being given. Detailed data regarding rates of growth of trees seem to show that they are proportional to the heights of the various forest types. Stations were located in these forests, and at them measurements were made of environmental factors, including temperature, light, evaporation, rainfall, humidity, soil moisture, and wind velocity. Many data were collected and are presented in tables and graphs. Some of the most interesting conclusions based upon these are: (1) humidity is high at all elevations, and the atmosphere is practically saturated at all times under the montane forest; (2) temperature gradually decreases with rising elevation; (3) evaporation in all forests is much less than in the mesophytic forests of the United States, and decreases rapidly with increasing altitude; (4) there is a pronounced, although not severe, dry season; (5) only at low elevations does there appear to be sufficient decrease in soil moisture during the dry season to have any harmful effect on vegetation; and (6) the increase in her-

baceous vegetation with increasing altitude is due to increased soil moisture and decreased rate of evaporation.

An analysis of the foliage shows that leaves with entire margins are more abundant in the lower stories than in the upper, and at lower elevations than at higher ones. Classified according to the system devised by RAUNKIAER, the plants over a meter in height are found to show but three leaf sizes, and the number of species with microphyll, mesophyll, and macrophyll leaves are, for the most part, Dipterocarp forest, respectively 4: 79: 9; for the mid-mountain forest 4:61:5; and for the mossy forest 8:8:0, showing a decided decrease in leaf size with increase in elevation.

The Philippine vegetation is made more attractive to the reader by numerous good photographs reproduced on excellent plates.—GEO. D. FULLER.

Transpiration studies.—A series of papers by SAYRE[9] contains some interesting results regarding transpiration from hairy leaves. The leaves of the mullein, *Verbascum Thapsus*, offer more resistance to water loss in darkness than in light, in still air than in wind, and respond rather more to changes in environment than do the smooth leaves of tobacco, *Nicotiana* sp. The removal of the hairs of the mullein leaves resulted in no change of resistance in still air and light, and but slightly reduces resistance in wind and light. There was a greater reduction of resistance to water loss caused by the removal of hairs in still air and darkness, as under such conditions transpiration is entirely cuticular. Hence it appears that, in this plant at least, hairs as a covering affording protection against ordinary intensities of wind and light are quite inefficient and may be disregarded. The stomatal water loss is 20–40 times the cuticular, and only the latter is influenced by the removal of the hairs.

Transpiration, humidity, evaporation, and sunshine were recorded along with the water loss from sealed potted plants. Stomatal transpiration is shown to be governed by various factors which control the opening and closing of the stomatal pores, and by the diffusion gradient. An increasing saturation deficit of the intercellular spaces of the mesophyll is regarded as important in increasing the resistance of the leaf to water loss while stomata are open, but as of no effect after stomata are closed by darkness.

The tobacco and *Verbascum Thapsus* show a rhythm in the transpiration curve in darkness for one day only succeeding a day of normal light exposure, but *V. Blattaria* exhibits no such rhythm under the same conditions.—GEO. D. FULLER.

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[9] SAYRE, J. D., Comparative transpiration of tobacco and mullein. Ohio Jour. Sci. **19**:422–426. *fig. 1.* 1919.

———, Factors controlling variations in the rate of transpiration. *Loc. cit.* **19**:491–509. *figs. 9.* 1919.

———, The relation of hairy leaf coverings to the resistance of leaves to transpiration. *Loc. cit.* **20**:55–75. *fig. 7.* 1920.

A new rubber.—HALL and GOODSPEED,[10] in connection with the war demand, have investigated a possible native source of rubber, studying especially *Chrysothamnus*. They found rubber of high grade in *C. nauseosus*, and adopted the name "chrysil" for this particular kind or rubber. This species includes 22 recognized varieties, which have been taxonomically presented by HALL.[11] Of these varieties, 12 were examined and all found to contain rubber. The shrub grows readily from seed and matures in 6–8 years. The largest stands occur in Colorado, Nevada, and Utah; and it is estimated that the total amount of rubber present in wild shrub is over 300,000,000 lbs.

Chrysil is not a latex rubber, but occurs in individual cells. The results of 180 chemical analyses and 80 microscopical examinations are tabulated. The rubber occurs in the plants in greatest abundance about the soil line, being present in the root in only the upper parts, and occurring in small amounts in young twigs and leaves. The best varieties for rubber are those growing in alkaline soils, so that the culture of this rubber-yielding plant could be developed extensively in alkaline regions unsuitable for other crop plants.

The authors[12] also give an account of the occurrence of rubber in other species of *Chrysothamnus* and in *Haplopappus*. They also append a long list of species, chiefly Compositae, in which no rubber was found.—J. M. C.

Philippine bamboos.—In a recent bulletin BROWN and FISCHER[13] have presented much interesting data regarding the taxonomy, ecology, and economic value of Philippine bamboos. Nine genera, including 30 species, 17 erect and 13 of climbing habit, are described, and a key for identification is provided. Planting and harvesting methods are discussed, and some data regarding market prices given; but of much more interest to ecologists is a series of accurate growth records extending over a period of 20 weeks. Growth rates of 2 m. per week are not uncommon, and several shoots showed a weekly growth in excess of 3 m.—GEO. D. FULLER.

Salix.—SCHNEIDER,[14] in continuation of his studies of American willows, has discussed the section Adenophyllae, recognizing 8 species, one of which (from California) is described as new. The discussions and descriptions are very full, and are accompanied by complete citations of collections, so that taxonomists will be at no loss as to the plants referred to.—J. M. C.

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[10] HALL, H. M., and GOODSPEED, T. H., Chrysil, a new rubber from *Chrysothamnus nauseosus*. Univ. Calif. Publ. Bot. 7:183–264. *pls. 18–20. figs. 6.* 1919.

[11] HALL, H. M., *Chrysothamnus nauseosus* and its varieties. *Idem* 7:159–181. 1919.

[12] HALL, H. M., and GOODSPEED, T. H., The occurrence of rubber in certain west American shrubs. *Idem* 7:265–278. *figs. 2.* 1919.

[13] BROWN, WM. H., and FISCHER, A. F., Philippine bamboos. P.I. Dept. Agric. and Nat. Res., Bur. For. Bull. 15: pp. 32. *pls. 33.* 1918.

[14] SCHNEIDER, CAMILLO, Notes on American willows. VII. Jour. Arnold Arboretum 1:147–171. 1920.